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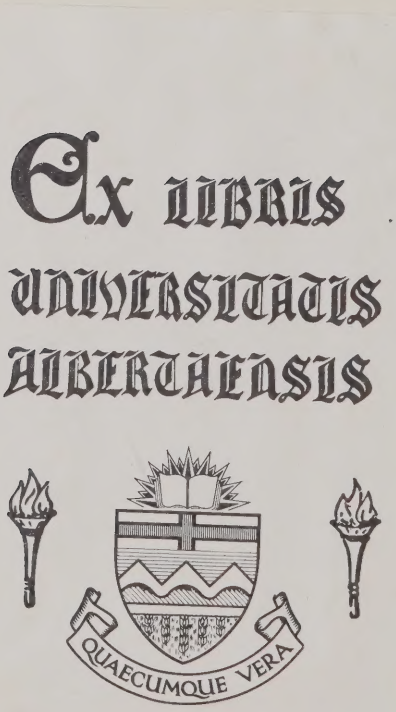

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AN ECOLOGICAL STUDY OF THE BASOMMATOPHORAN SNAIL *HELISOMA TRIVOLVIS* IN CENTRAL ALBERTA

by

© J. ROBERT MORRIS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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ABSTRACT

A population of *Helisoma trivolvis* (Planorbidae, Planorbinae) in an artificial pond in central Alberta was studied in 1968 and 1969. These snails could be aged by counting the "rest lines" produced annually on their shells, and while some individuals had survived four or five years, adult snails were mostly one year old. Shell growth occurred during the spring. The population was distributed largely within about 20 feet from shore. Adults gradually moved nearer the shore during spring and summer, but apparently retreated to deeper water before autumn. Juveniles (newly hatched snails over 2.0 mm in diameter) were concentrated between 1.5 and 4.5 feet from shore through July, but became less concentrated and began moving away from shore in August. Larger juveniles were found farther from shore than smaller specimens. The Abundance Index (mean number per transect, covering 10 sq ft) of adult snails increased from 15.2 in May 1968 to 44.0 in May 1969, but declined drastically by the end of 1969 after an almost total loss of juveniles. Juveniles had a maximum Abundance Index of 209.2 in August 1968. The Abundance Index of adult snails declined to less than unity during both summers. Spawning occurred in the spring and early summer. Egg masses, containing 10 to 68 eggs, were deposited near the bottom of the pond on dead vegetation, rocks and the shells

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of living snails. Eggs deposited on Plexiglas substrates (described) were utilized in determining that spawning occurred earlier at locations nearer the shore, and that rising water temperature stimulated spawning while decreasing temperature had depressive effects. Spawning could not be artificially induced in the laboratory by warm temperatures and long-day photoperiods. After juvenile snails exceeded 8 to 9 mm in diameter, their rate of growth decreased and reproductive maturation began. Some juveniles attained this size by mid-July and nearly all did so by September. Up to 34 per cent of the adult snails were infected by the rediae of *Echinoparyphium recurvatum*, an echinostome trematode. These rediae destroyed the ovotestis, albumen gland and digestive gland of their hosts, causing their castration and death. The metacercariae of this trematode encysted in the kidney of *Helisoma trivolvis* and may have caused heavy mortality in newly hatched juveniles in 1969. Its major definitive host was the blue-winged teal (*Anas discors*). Population interactions among *Helisoma trivolvis*, *Echinoparyphium* and blue-winged teal were discussed with emphasis upon the effects of snail density. Extensive data on water temperatures were obtained, and an apparatus was designed to collect water samples in a syringe for dissolved oxygen analysis.

ACKNOWLEDGEMENTS

I am particularly indebted to Dr. D. A. Boag, my supervisor, for the encouragement, support and well considered advice which he provided generously whenever the need arose. To him I express my deepest gratitude.

The valuable advice and direction given by the other members of my advisory committee, Dr. W. G. Evans, Dr. H. F. Clifford and Dr. J. C. Holmes, were also greatly appreciated.

I am obliged to Mr. R. Shank for allowing me to carry out my field investigations on his property. Also, Dr. W. G. Evans, of the Department of Entomology, Dr. D. D. Beatty and Mrs. V. Scott, of the Department of Zoology, and Mr. H. Welling, of the Greenhouse Department, generously made available facilities and equipment used in experiments on the effects of temperature and photoperiod.

Special thanks are due also to Dr. J. C. Holmes and Mr. R. Podesta who identified the parasites I encountered, and patiently discussed trematode biology with me on numerous occasions.

I was fortunate to have the aid of two student assistants, Mr. R. Forbes and Mr. L. Noton, during the summers of 1968 and 1969 respectively. Without their responsible efforts, the field studies could not have been carried out.

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INTRODUCTION

Ecologists are beginning to consider the possibility of constructing new, stable communities and ecosystems, designed specifically to meet the needs of mankind (Odum, 1969). But our understanding of the components available, that is, our ecological knowledge of specific organisms, is generally inadequate.

Despite their medical-parasitological importance, wide distribution, and prominence in the aquatic environment, the freshwater snails are among those animals whose ecology is poorly understood.

Mozely (1954:38) commented that "in earlier days it was taken for granted that all bodies of water are inhabited by dangerous species of snails. Now it has been found that they are markedly restricted in their occurrence. But the old legend dies slowly."

This study was stimulated by a similar observation, that, in central Alberta at least, certain basommatophoran gastropods were to be found in but a fraction of the numerous, apparently suitable, habitats present. Furthermore, an analysis of the suitabilities of a large number of ponds, judged on the basis of what was known of snail biology, provided no obvious explanations for the distribution of snails among them.

It seemed, therefore, that a prerequisite for

understanding snail distributions was a more adequate knowledge of the biology of individual species.

With this in mind, a study was initiated in 1968 on an established population of *Helisoma trivolvis* (Planorbidae, Planorbinae) in an artifical pond situated fifty miles north of Edmonton, Alberta. Of primary concern were the questions "Where does this snail live within this pond?","What are the characteristics of its habitat?", "How, when and where does it reproduce?", "What factors contribute to its mortality?", and "What changes occur in the structure of this population within and among years?".

STUDY AREA

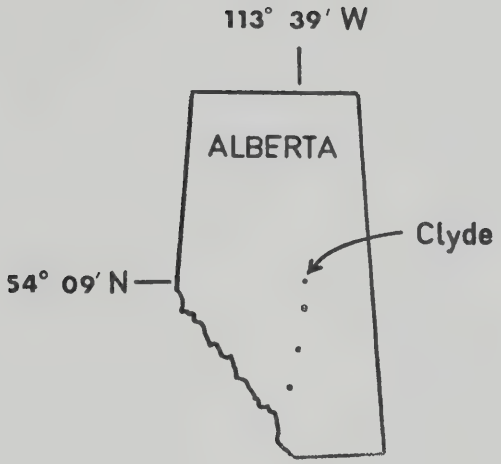
A permanent man-made pond (Clyde Pond), located in central Alberta near the village of Clyde, was the site of field investigation and the source of *Helisoma trivolvis* specimens used in the laboratory (Fig. 1 and 2). This pond, situated near the northern edge of the parkland, was surrounded on two sides each by cultivated land and tame hay. It had been excavated in June 1960.

In 1968 emergent vegetation in Clyde Pond was restricted to a few small stands of *Typha latifolia*. Submerged vegetation was present as a narrow band near the shore consisting of heavy growths of *Myriophyllum exalbescens* and scattered clumps of two unidentified species of *Potamogeton*. Most of the *Typha latifolia* was dead by the middle of the summer of 1969 as a result of lowered water levels. *Myriophyllum exalbescens*, on the other hand, had spread by this time across the entire pond.

In 1968, its snail fauna consisted of relatively abundant *Helisoma trivolvis*, a much smaller number of *Physa gyrina*, and a very few *Lymnaea stagnalis* and *Stagnicola palustris* (lymnaeid nomenclature according to Inaba, 1969). Judging by the empty shells found, *Stagnicola palustris* had been abundant in previous years, while *Lymnaea stagnalis* had probably been rare or absent.

Also numerous in this pond were insect larvae, particularly Tendipedidae, cladoceran and amphipod crustaceans, and oligochaetes. Small fish *Culaea inconstans* and *Pimephales promelas* and an ectoproct *Plumatella repens* were abundant in 1968, but not in 1969.

Figure 1. The location and physical features of Clyde Pond.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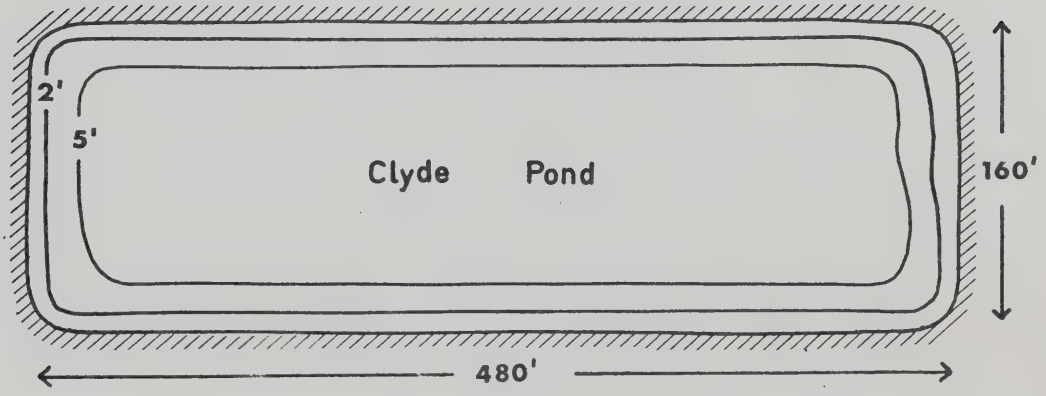
ALBERTA
Clyde
54° 09′ N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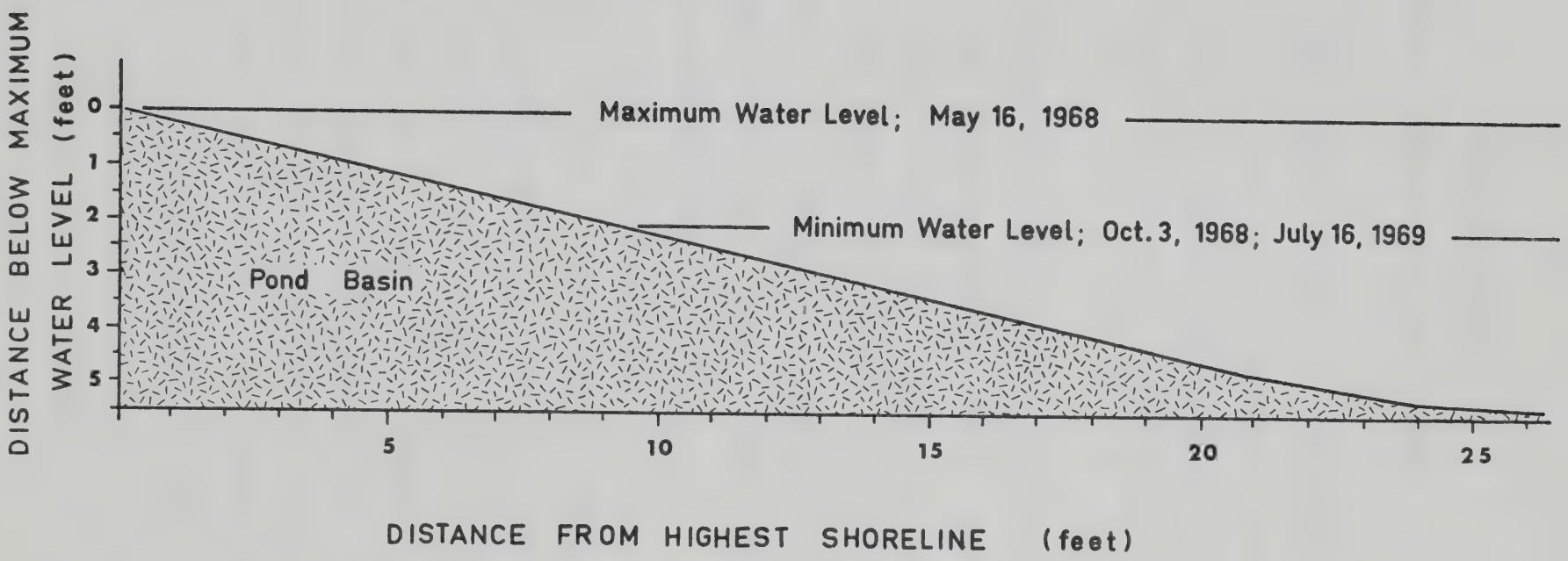
5′
Clyde Pond
160′
480′

Figure 2. The bottom profile along the sides of Clyde Pond, and the positions of the maximum and minimum recorded water levels.


DISTANCE BELOW MAXIMUM WATER LEVEL (feet)
0
1
2
3
4
5
Maximum Water Level; May 16, 1968
Minimum Water Level; Oct. 3, 1968; July 16, 1969
Pond Basin
5
10
15
20
25
DISTANCE FROM HIGHEST SHORELINE (feet)

GENERAL METHODS

Physical and Chemical Features of Clyde Pond

A stake was driven firmly into the bottom of the pond at the start of the study. At intervals thereafter, changes in water level were determined by measuring the distance from the water's surface to a reference point on this stake.

Dissolved oxygen concentrations were determined in water samples taken several times in 1968, and at various locations, one of which was always near the middle of the pond. On each occasion, a sample was collected at the water's surface and at one-foot intervals down to about one inch from the bottom. Burke's (1962) modification of the Winkler method was followed .

In this "micro" technique, most of the reactions occur within a 10 ml syringe; a new piece of equipment was devised (APPENDIX I) which made it possible to take water into the syringe directly at any desired depth. In preparation for sampling, the syringe (a) was placed in the sampler and held in position by rubber bands(b). The plunger of the syringe (c) was then pressed tightly against the end of the syringe barrel by raising the slide (d) of the locking mechanism, and the heavy rubber band (e) was attached to the end of the plunger. The removal of all air bubbles from the syringe was facilitated if

the syringe was wet.

A water sample was obtained by lowering the readied apparatus to the desired depth (marked on the cord (f)) and then releasing the messenger (g) to travel down the cord. The messenger, striking the slide of the locking mechanism, causes the syringe plunger to be released and pulled upward by the rubber band (e) thus drawing the water sample into the barrel of the syringe. In shallow water at least, it is convenient to replace the cord with the probe cable of an electronic thermometer. The position of the probe may be adjusted so that the temperature is obtained exactly in the stratum of water being sampled.

After the water sampler has been retrieved, the elastic bands holding the syringe are removed and the syringe containing the water sample may be lifted from the sampler.

The Calcium hardness and the pH of the water were determined using a Hach DR-EL portable analysis kit.

On most visits in 1968, water temperatures at the surface and at one foot intervals down to the bottom were recorded near the middle of the pond. This was always done when dredge sampling or dissolved oxygen analysis was carried out.

In 1969, a Ryan thermograph, stationed about 12 feet from shore and 15 inches beneath the water's

surface (Station A) provided a continuous record of water temperature from April 28 to September 15. A second thermograph was stationed on the bottom, directly below the first (Station B), from July 9 to August 17. Water temperatures were also taken periodically at the bottom of the pond at selected distances from shore, and at one-foot intervals from the surface to the bottom in the vicinity of the thermographs.

Distribution and Age Structure of the Snail Population

Data on the composition of the *Helisoma trivolvis* population, and its distribution within the pond, were obtained primarily by systematically sampling the pond bottom at least once per month during ice-free periods in 1968 and 1969. In some instances, to be noted later, these data were supplemented by observations on snails collected by hand or dip net.

For bottom sampling, transects were established by stretching a nylon rope tightly across the width of the pond. A six-inch-square Ekman dredge was operated from an inflated rubber dingy, which was moved along these transects to the required sampling points. Sampling and the measurement of water depth began at the water's edge and continued at pre-determined intervals along the transects. Initially, samples were collected at three-foot intervals, but later, as the snails appeared to be

concentrated near the shores, this spacing was reduced to 1.5 feet to improve collecting efficiency. Sampling series were terminated between 13.5 and 21 feet from shore, and generally from two to four series of samples were collected on each sampling date.

No transect was followed more than once to avoid any bias that might have appeared as a result of the disturbance of the bottom by previous sampling.

In 1968, dredge samples were transported in large plastic bags to the laboratory at Edmonton where they were washed and sorted over a series of screens, the finest of which had openings 0.75 mm square. The living snails, empty shells, and snail egg masses recovered were preserved (70 per cent ethanol and 5 per cent glycerine).

The maximum diameters of both inhabited and empty shells of *Helisoma trivolvis* collected were measured to the nearest tenth of a millimeter.

It was found that many snails less than 2.0 mm in diameter were unavoidably damaged in the sorting process. Therefore, this size class was disregarded, and in 1969 the dredge samples were sorted in the field over a single screen with 2.0 mm square openings. Live snails and empty shells were retained in 1969.

For a study of possible depth preferences in newly hatched snails, a column-like aquarium (48 inches tall by three inches square) was filled with water to a depth

of 45 inches, and kept at room temperatures (20-22°C) near a north window. This encouraged a sparse but more or less uniform growth of algae, and associated organisms on the aquarium walls. In mid-May, 12 *Helisoma trivolvis* snails were brought directly from Clyde Pond and accomodated in this aquarium for one day. The positions of all egg masses deposited were recorded.

The eggs were allowed to hatch, and the vertical distribution of the young snails was noted immediately after hatching. Such observations were continued at intervals for about two and a half months. No extra food was supplied.

Reproduction

The process of egg mass deposition by *Helisoma trivolvis* was observed in a transparent aquarium.

In 1968, the egg masses recovered from each dredge sample were counted, as were the eggs in each egg mass. The locations of the egg masses, in terms of water depth, distance from shore and substrate type, were also noted.

It was discovered in 1968 that Plexiglas introduced into the pond was acceptable to *Helisoma trivolvis* as a substratum for its egg masses. Thus, in 1969, "artificial substrates" of this material were placed in Clyde Pond to obtain information on how such factors as the time of year, water temperature, distance from shore

and the presence of other egg masses might influence such things as rate of oviposition, location of egg masses, and fate of the eggs.

Substrate units consisted of 1/8 inch thick pieces of Plexiglas, each one foot long by three inches wide, bonded together to form a one-foot-tall "box" with open ends three inches square. The surface of the Plexiglas was scored in a grid of one inch squares, so that egg masses could be recognized individually by their positions on the substrate.

In order to station substrates systematically at various depths and distances from shore, 12 two-inch-square wooden stakes were driven into the pond bottom in a row perpendicular to the shoreline. The first stake was placed about one foot from shore, where the water was initially three inches deep, and the others at intervals of 1.5 feet towards the middle of the pond.

An artificial substrate unit was then threaded over each stake and lowered carefully to the bottom by an attached nylon string. The substrates were in position before oviposition had begun, and they were examined to record both new egg masses, and the condition of previously-noted egg masses, up to three times weekly during the reproductive season.

When there were few egg masses per substrate, the total number of newly deposited eggs was determined by

counting them directly with the aid of a hand lens. Generally, however, egg masses were so numerous that this was not feasible, and the number of new eggs had to be determined indirectly as the product of the number of new egg masses and the mean number of eggs per new egg mass.

Two additional artificial substrates, situated several yards to one side of the original row of stakes, yielded egg masses which were removed each time the substrates were inspected, and taken to the laboratory for counting of the eggs.

In order to study reproductive maturation, juvenile and adult *Helisoma trivolvis* were removed from their shells, and their ovo-testes, seminal vesicles, and albumen glands were examined under a dissecting microscope. The state of ovo-testis development was judged by the prominence of the acini, while the criterion used for the albumen gland and seminal vesicles was relative size.

In mid-May 1969, spawning *Helisoma trivolvis* were collected and observed in the laboratory to determine the average rate of oviposition under controlled conditions. One hundred specimens were divided into groups of five, and placed in 20, numbered, one-gallon, plastic containers which had been perforated to allow the passage of water. Each of five 12-gallon aquaria held four of these containers.

The air temperature in the chamber holding these aquaria was set at 16°C, to correspond to prevailing temperatures in the pond, but the water temperature fluctuated diurnally within the range of 14.5°C to 18.5°C as a result of evaporative cooling and heating from the lights.

The photoperiod was set at from 0430 to 2030 hours, which corresponded to field conditions at the time of collection.

The snails were provided an excess of an artificial diet (Lee and Lewert, 1956) which had previously been found acceptable to this species.

Aquarium water was continuously aerated and passed through filters containing glass wool and activated charcoal.

Egg masses deposited in the containers were collected every two or three days.

To determine whether increasing and decreasing temperature regimes could respectively stimulate or depress egg production, 80 *Helisoma trivolvis* were taken from the pond on May 28, 1969, and added, in groups of 10, to eight plastic containers of the type described above. Two containers were placed in each of four aquaria. An excess of the artificial diet was provided throughout the experiment, and the aquarium water was aerated and filtered continuously.

The temperature in the pond had decreased from

about 19°C on May 25, to about 13°C on May 28. Thus, the first aquarium was held at 12.5-13.0°C for one week to investigate the effect of maintaining the temperature reduction which the snails had just experienced in the field. The temperature was then increased to 16.0-17.0°C for three days to discover whether the effect was reversible.

The second aquarium was maintained at 19.0-20.5°C for one week to demonstrate the effect of rapidly increasing the temperature by 6°C, to its previous high level of May 25.

The third and fourth aquaria were held at 15.0-18.0°C for five days, and then the fourth was warmed to 18.0-19.0°C for two days. This demonstrated the effect of increasing the temperature by 3°C, and of increasing it by 6°C in two steps of 3°C each.

The numbers of egg masses and eggs deposited in the eight containers were recorded.

Another series of experiments was carried out to determine whether, and at what time, spent *Helisoma trivolvis* would begin to spawn again if kept under more or less constant conditions in the laboratory, and whether snails from the pond could be induced to spawn in the fall by bringing them to warmer conditions in the laboratory in fall or late summer.

Firstly, 50 specimens were collected in June

1969, and divided into two groups to be maintained as long as possible, one at 15-18°C and the other at 22-25°C. The photoperiod was maintained between 15 and 16 hours. The water was continuously aerated and filtered, and a steady though not always excess supply of artificial food was provided.

Secondly, six to eight snails were collected weekly from August 11 to September 1, 1969 and kept at room temperature, in culture dishes, with an excess of artificial food until mid-September. Any evidences of copulation or spawning were recorded.

In order to test whether a period of cold or freezing temperatures followed by warming was necessary to permit spawning, 60 *Helisoma trivolvis* were obtained from Clyde Pond on October 5, 1969, and assigned in equal numbers to five treatments. In the "control" treatment, 12 snails were held at 18-19°C for the duration of the experiment (5 months). In the remaining four treatments, the snails were subjected for one week, or for one month, to either 2-6°C or 0-3°C (temperatures near the lower extremes of these ranges were in effect most of the time). After their cold treatments, the snails were warmed and maintained at 18-20°C until March 1, 1970 when the experiment was terminated. Examinations for egg masses were made regularly throughout the experiment, and a steady supply of artificial food was provided.

Mortality Factors

Helisoma trivolvis was subjected in the laboratory to instantaneous changes in temperature of up to 12°C, both warming and cooling, within the range of 4 to 20°C. The snails were maintained at the new temperatures for at least one week. Other snails were subjected to 0°C for various periods up to three days, or to freezing in ice for 24 hours; they were then warmed enough to allow activity. Snails were considered to have died when they showed no spontaneous movements, or no response to a pin-prick.

Specimens of the fish present in Clyde Pond were collected and identified, and their stomach contents were examined for the remains of snails.

Specimens of each species of the tabanid larvae (Diptera) and leeches found in the pond were maintained in small dishes, in association with specimens of *Physa gyrina* and *Helisoma trivolvis* for two weeks. Any evidence of predation on the snails was noted.

Helisoma trivolvis recovered by dredging in both years, and many of the snails used in the laboratory, were examined to evaluate both the incidence of trematode parasites, and their effects on their snail hosts. All snails found to be infected by rediae (from all collections) were classified as lightly, moderately, or heavily infected. The location of the rediae, as observed using a dissecting microscope, was also recorded in each case. These data

described the progress of redial infections in terms of both the order in which various organs were attacked, and the time of year. The occurrence of metacercariae also was recorded.

An attempt was made in the laboratory to follow the complete life cycle of the trematode found.

Statistical Analysis

Wherever there were sufficient numbers of observations, the data obtained in this study were plotted as frequency distributions to determine whether they could be analysed by "parametric" statistical tests. In every case examined, the populations to be tested violated the required assumptions. That is, the frequency distributions were not "normal" distributions and/or the variance was not homogeneous among treatments. In view of this, "distribution free" statistical tests were employed in all analyses. The Kruskal-Wallis Rank Sum Test (Bradley, 1968:138-141) was applied to multi-population comparisons, and the Wilcoxon Rank Sum Test (Bradley, 1968:105-114) to two-population comparisons. Both tests are valid regardless of the distribution of observations, and under normality are only slightly less powerful (Asymptotic Relative Efficiency = 0.955) than their parametric counterparts, the F and t tests (A.R.E. = 1.000) (Bradley, 1968:60).

RESULTS AND DISCUSSION

Physical and Chemical Features of Clyde Pond

There was a difference of 25 inches between the maximum and minimum levels of the surface of Clyde Pond during the period of study (APPENDIX II). The substantial declines in water level following August 13 and September 11 in 1968 resulted from water being pumped out of the pond for use in highway construction. The rise in water level following August 21, 1968, was the result of water being added from another pond nearby.

The apparatus used to obtain water samples for dissolved oxygen analysis (APPENDIX I) eliminated the need to transfer the samples from a collecting bottle to the test vessel. Thus, the likelihood of sample contamination was greatly reduced, and tests could be completed more quickly. This apparatus also made it possible to define within an inch the depths from which samples were recovered. Schindler (1969) has also described a device for collecting water samples in a syringe, but because the barrel of the syringe moves downward as the syringe fills, his apparatus does not sample a single stratum of water. Also, the syringe is not as conveniently removed from his sampler as from the presently described apparatus.

The data obtained on dissolved oxygen concentra-

tions are listed in APPENDIX III. Above a short distance from the pond bottom, the per cent saturation was always relatively high. However, during the night of July 25, 1968, oxygen was substantially depleted at the pond bottom. Because this night had been both warm (APPENDIX V) and calm, the recorded value of 3.0 ppm was probably very near the minimum value for the summer.

Since the genus *Helisoma* is resistant to anaerobic conditions (von Brand, McMahon and Nolan, 1955), the *Helisoma trivolvis* population in Clyde Pond was expected to tolerate depletion of oxygen in winter. This expectation apparently was borne out since *Helisoma trivolvis* survived the winter of 1968-69, while the brook stickleback (*Culaea inconstans*) and the fathead minnow (*Pimephales promelas*) did not.

It has long been known that soft water environments are inhabited by few snails (Pennak, 1953). Van der Borght and Van Puymbroech (1966) have explained this fact by showing that 80 per cent of the calcium fixed by *Lymnaea stagnalis* was derived directly from the surrounding water.

Calcium hardness and pH measurements are given in Table 1 for Clyde Pond and other artificial ponds in central Alberta. The ponds near Fox Creek were about 140 miles west of Clyde. A few empty shells, but no living snails were found in ponds B and C. About three quarters

Table 1. Calcium hardness and pH recorded in artificial ponds in central Alberta.

Pond	Location	Date	Calcium Hardness (as $CaCO_3$) ppm	pH
Clyde Pond	Clyde	16/5/68	25	9.4
B	Clyde	22/5/68	80	8.2
C	Clyde	27/5/68	50	9.2
Forty Ponds	Fox Creek	mid-summer 1967	Mean: 64 Range: 23-110	Mean: 9.1 Range: 8.4-10.1

of the Fox Creek ponds supported populations of one or more species of basommatophoran snails, but there was no apparent relationship between the occurrence of snails and either calcium hardness or pH (APPENDIX IV). It seemed unlikely, therefore, that the distribution of snails among ponds in central Alberta was significantly restricted by calcium concentrations.

The Clyde Pond water temperatures were found to fluctuate markedly, in time and from place to place (see APPENDICES V to VIII). Such variability apparently resulted from complex interactions among many factors, and though these factors were not investigated specifically, an impression was gained as to the identities and roles of the more significant among them.

Bright sunshine seemed to be the most important agent in warming the water, and where the water was more than a few inches deep, it contributed to the production of vertical temperature gradients. Strong winds, on the other hand, tended to mix the waters and obliterated such gradients. Wind, in tending to increase evaporation from the water's surface, will also have had a cooling effect. Aquatic vegetation exerted a major influence by shading the deeper water and presumably by retarding mixing. It thus accentuated and tended to stabilize vertical stratifications.

Lateral temperature gradients were almost always

found (APPENDIX VI) with the warmest water being near the shore, and it was assumed that these were primarily a function of water depth. The distances from shore selected for these temperature measurements were such that temperatures were recorded beside the stakes which held the Plexiglas subtrates (p.12).

Water temperature changes recorded in 1969 at thermograph Stations A and B are given in APPENDICES VII and VIII. It was decided to characterize daily temperature regimes by the values recorded at 0600, 1200, 1800 and 2400 hours.

From 1800 of July 29 to 0600 of July 30, 1969, thermal stratification at the thermograph stations was the inverse to the usual situation, with the warmer water being nearer the pond bottom. This situation appeared several times when rapid cooling was taking place, but it was always short lived. Young and Zimmerman (1956), who first recorded such inversions in a shallow pond, also associated them with an abrupt change from warming to cooling conditions.

At Station A, the 0600 hours temperature was generally the lowest and the 1800 hours temperature the highest each day (Fig. 3 and 4). Also, the daily maximum and minimum temperatures were always closely approximated by at least one of these four temperatures. At Station B, daily temperature fluctuation was much less marked than at

Figure 3. Relationships between the time of day and the occurrence of the daily maximum and minimum water temperatures at thermograph Station A, (15 inches below the water's surface) April 29 to September 14, 1969.

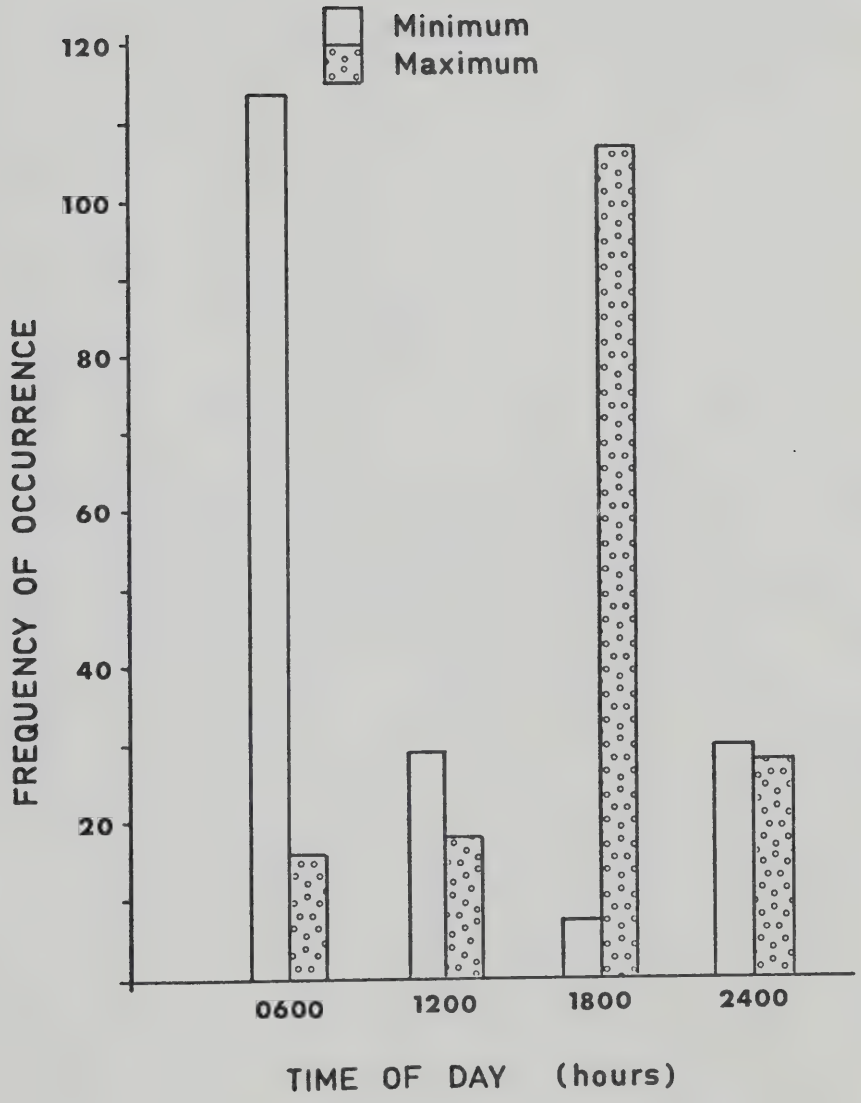
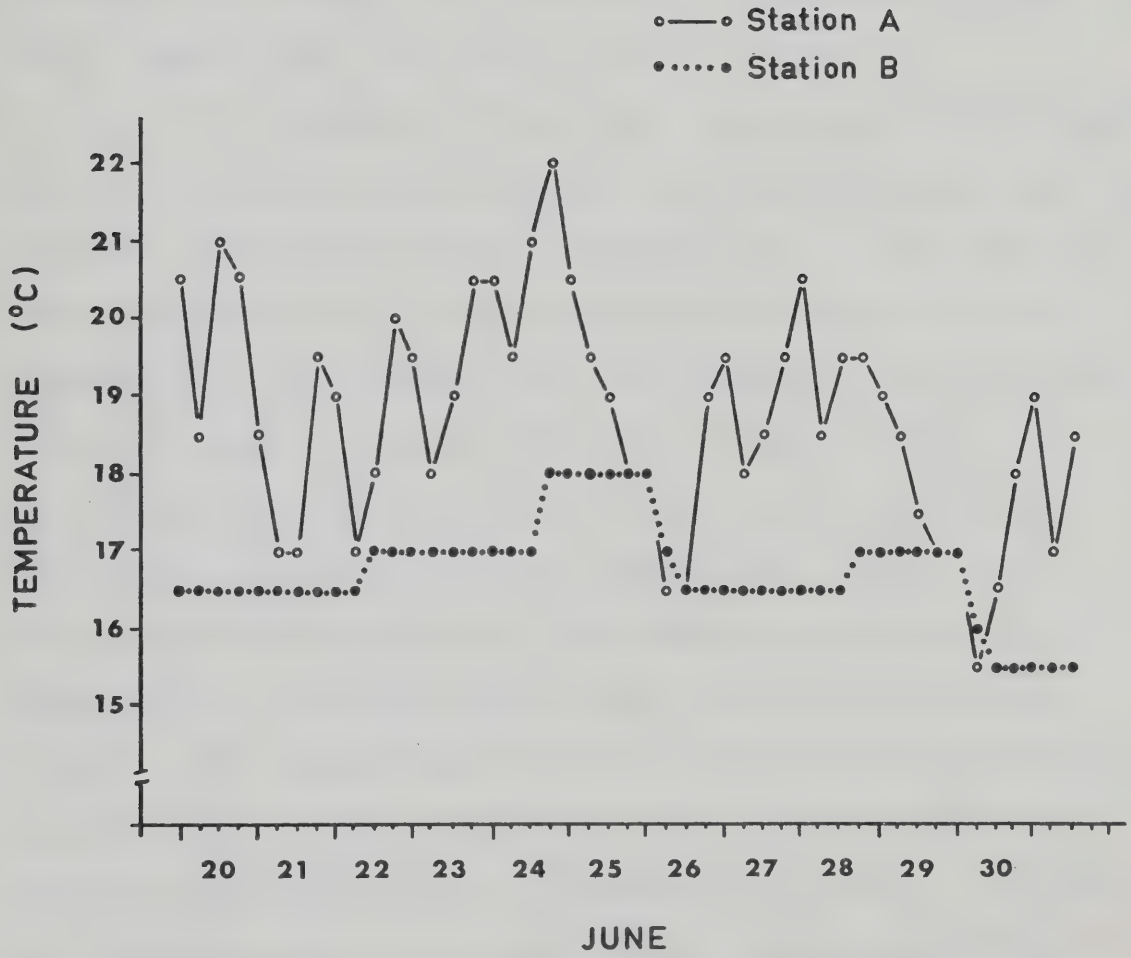

Minimum
Maximum
120
100
80
60
40
20
FREQUENCY OF OCCURRENCE
0600
1200
1800
2400
TIME OF DAY (hours)

Figure 4. Daily temperature fluctuations typical of thermograph Stations A (15 inches below the water's surface) and B (at the pond bottom).

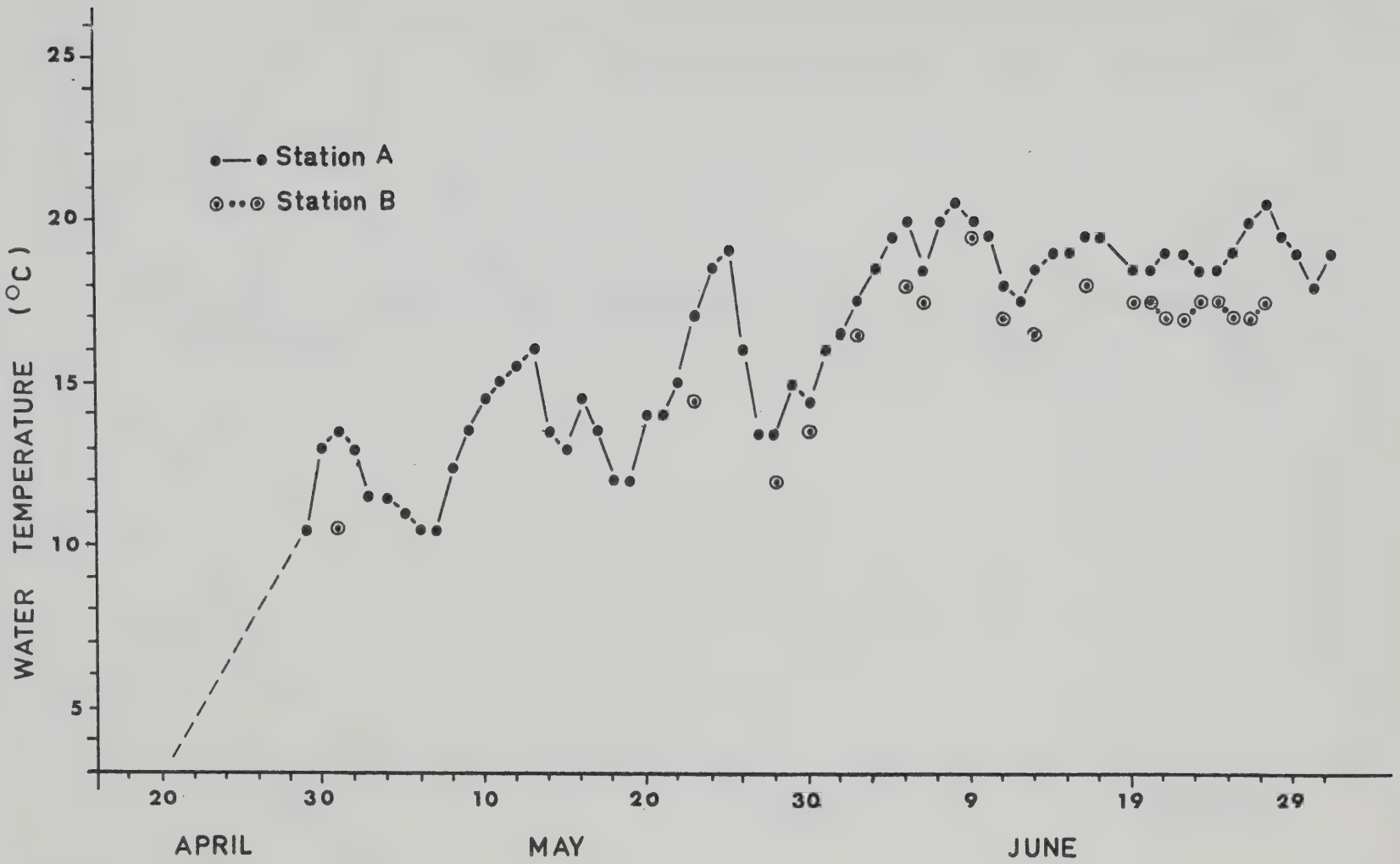

Station A
Station B
TEMPERATURE (°C)
22
21
20
19
18
17
16
15
20
21
22
23
24
25
26
27
28
29
30
JUNE

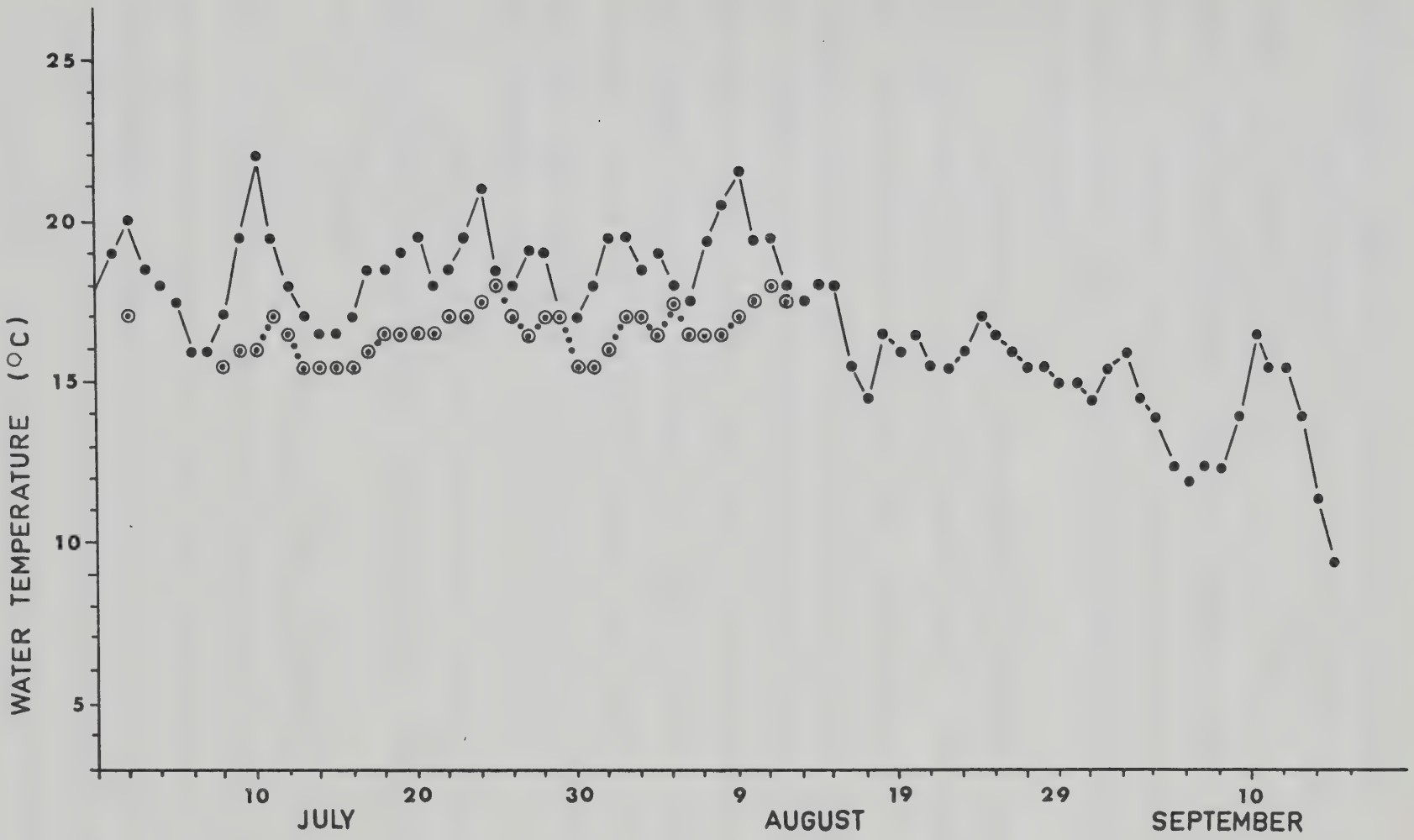
Station A (Fig. 4); a change of more than one degree Centigrade per day was rare and changes lagged those at Station A by 12 hours or more.

The four temperatures recorded daily at each thermograph station were averaged and considered as mean daily temperatures for these locations (Fig. 5).

In composite, these data demonstrated that temperature profiles in shallow waters are often complex, and that they are furthermore almost constantly in a state of flux. They emphasize that extreme care must be exercised both in interpreting temperature data ecologically, and in planning when and where to record such data. Reid's (1961) text is almost alone in considering even briefly temperature conditions in shallow waters. He pointed out (p. 121) that "Microthermoclines and odd temperature stratifications exist in certain small bodies under given conditions". This should not, however, be interpreted to mean that only the stable epilimnion-thermocline-hypolimnion type of stratification is significant or normal. In fact, in a shallow water environment, where rapid and profound changes in temperature apparently occur many times in a summer, the "odd" temperature conditions, though difficult to investigate, may well be ecologically the most significant.

Figure 5. Mean daily temperatures at thermograph Stations A (15 inches below the water's surface) and B (at the pond bottom) during the summer of 1969.


Station A
Station B
WATER TEMPERATURE (°C)
25
20
15
10
5
20
30
10
20
30
9
19
29
APRIL
MAY
JUNE


WATER TEMPERATURE (°C)
25
20
15
10
5
10
20
30
9
19
29
10
JULY
AUGUST
SEPTEMBER

Distribution and Age Structure of Snail Population

The numbers of snails recovered from each dredge sample are shown in APPENDIX IX, along with the sampling dates, and the distances from each sampling point to the shore. "Juvenile snails" were those hatched in the current season, while "adult snails" were those recruited in earlier years.

Variability in the spacing of sampling points, in the length of the sampling series, and in the numbers of series completed each day arose from several technical problems and from attempts to minimize the time expended in sampling areas of relatively low snail density. While some errors in judgement were made in this regard (for instance, the series on August 13 and August 21, 1968 ideally should have extended further from shore), the resulting bias towards underestimation of snail densities was probably small.

Heavy transverse "rest lines" (Baker, 1928) were observed regularly on the shells of all species of snails collected.

Orton (1923) was the first to suggest that "rings" on the shells of molluscs were indicative of the cessation of growth over winter, and that they could be used in age determination. There has been much difference of opinion concerning this technique and its value apparently varies with the species, the locality, the moisture conditions,

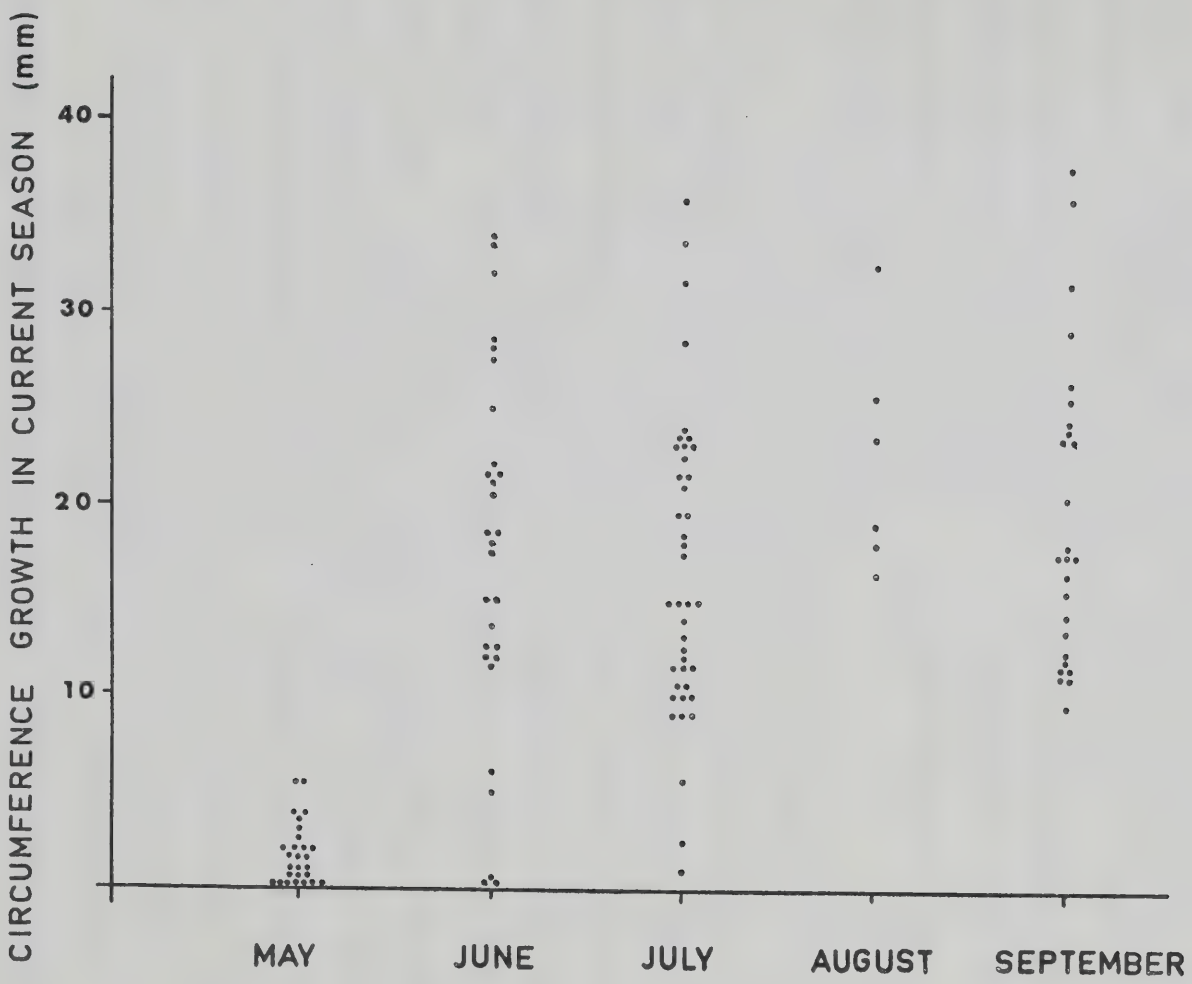
and possibly other factors as well (Comfort, 1957). To test its applicability to the present study, the distance from the last rest line to the lip of the shell was plotted against month of collection for *Helisoma trivolvis* specimens from Clyde Pond (Fig. 6). Snails obtained both by dredging and by hand collecting were utilized, but those parasitized by trematode rediae (see p. 80) or otherwise obviously abnormal were disregarded.

When all five months were considered, the distances from the lip of the shell to the last rest line were significantly different among months ($P_o < 0.01$, where P_o represents the probability that the null hypothesis of no difference was true). This suggested that the shells had lengthened significantly between the early spring and the fall. Since there were, however, no significant differences in shell growth among June, July, August, and September ($P_o > 0.05$) most, if not all, of the growth had occurred in May or early June.

A thickening of the lip of the shell, which began to appear in the late summer, was the only evidence of rest lines found on juvenile snails. Similarly located, but more pronounced thickenings were evident on virtually all snails collected in the fall and early spring.

It was concluded from these observations that one rest line was produced per year in Clyde Pond, and

Figure 6. Growth in circumference throughout the summers of 1968 and 1969 (distance from the last rest line to the lip of the shell) for adult *Helisoma trivolvis* collected in Clyde Pond.


CIRCUMFERENCE GROWTH IN CURRENT SEASON (mm)
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPTEMBER

that the number of rest lines on the shell was indicative of the number of summers survived.

When the number of rest lines on the shells *Helisoma trivolvis* was investigated, it was found that while their maximum life span was about four years, most of the adult population was one year old (Fig. 7). These data also suggested that relatively few snails had been recruited in 1966, or else such snails had survived rather poorly after recruitment. The former possibility seemed probable since evidence was obtained in 1969 that recruitment could be strongly depressed through high mortality of juveniles (p.88).

The empty shells from adult *Helisoma trivolvis* (unlike those of the juveniles) could persist intact in Clyde Pond for two years or more. If the shells from dead adults of different ages were uniformly likely to be collected, and had a uniform rate of decomposition, the age-at-death for shells (Fig. 7), determined by counting the rest lines, would indicate the "average" proportions of the adult population that died at each age. If these shells may be considered representative of a totally dead cohort hatched in a single season, these data also reflect the "average" age structure of the adult portion of the population.

Regarding maximum life span, these data were somewhat at odds with reports in the literature. Maximum life spans previously reported for several basommatophorans are listed in Table 2, and Hyman (1968:

Figure 7. The age structure of the adult population of *Helisoma trivolvis* in Clyde Pond. The majority of the empty shells were collected in May 1968.

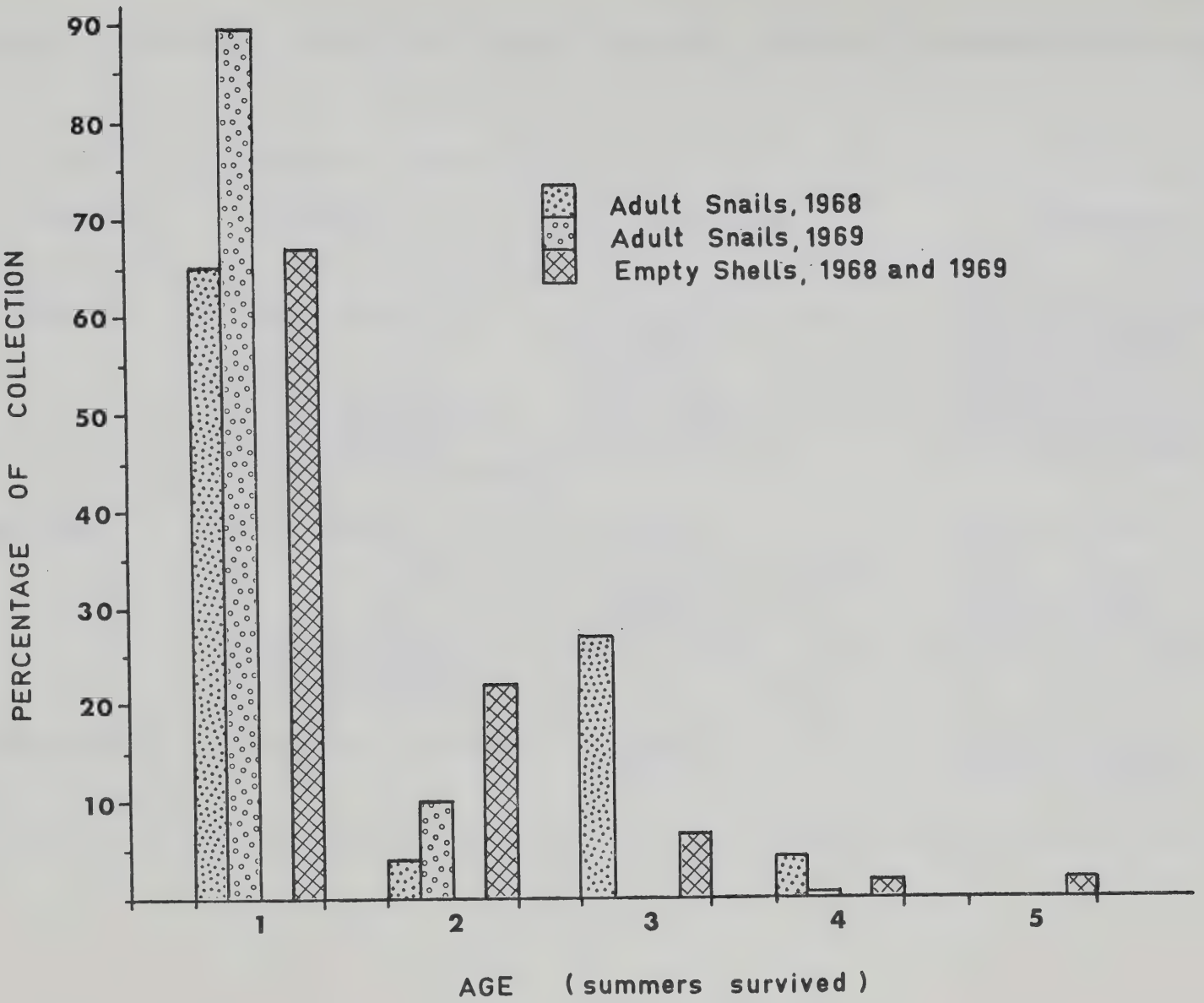

90
80
70
60
50
40
30
20
10
PERCENTAGE OF COLLECTION
Adult Snails, 1968
Adult Snails, 1969
Empty Shells, 1968 and 1969
1
2
3
4
5
AGE (summers survived)

Table 2. Reported normal life spans of several species of basommatophoran gastropods.

Family	Species	Life Span	Reference
Lymnaeidae	*Lymnaea stagnalis*	14 months (in lab.)	Noland and Carriker (1946)
	" "	25 months	Hunter (1961b)
	" "	2 years	Berrie (1965)
	Lymnaea humilis	9 months	McCraw (1961)
	Lymnaea emarginata	13-16 months	Howard and Walden (1965)
	Lymnaea elodes (*Stagnicola palustris*)	1-2 years	Eisenberg (1966)
Physidae	*Physa gyrina*	1 year	DeWitt (1955)
		22 months (in lab.)	
	Physa fontinalis	1 year	DeWit (1955)
	" "	1 year	Duncan (1959)
	Physa ampullacea	13-16 months	Howard and Walden (1965)
	Physa coniformis		
	Physa occidentalis		
Planorbidae	*Planorbarius corneus*	3 years	Boycott (1936)
	" "	2 years	Hunter (1961b)

613) has concluded that "most freshwater pulmonates live about one year". (Pulmonata has been abandoned in favour of Basommatophora (Taylor and Sohl, 1962) as the name of this taxonomic order.) This discrepancy may have meant that *Helisoma trivolvis* is longer lived than most basommatophorans, but, since a few specimens of *Lymnaea stagnalis*, *Stagnicola palustris* and *Physa gyrina* were also found near Edmonton with four or five rest lines on their shells, other explanations must be examined as well. Except in the laboratory investigations, where the ages of snails were known exactly, the age criterion used to obtain the information in Table 2 was merely the size of the shell. In Clyde Pond, one-year-old *Helisoma trivolvis* were often found which were larger than some three-year olds. Thus some of the data in Table 2 may be biased, and the values may approximate modal rather than maximum life spans of adults. On the other hand, Comfort (1957) has suggested that the rate of ageing of snails may be modified by both nutrition and temperature. Snails may simply be long lived in central Alberta because of the cool climate and long winters.

It was logistically impossible to carry out a sufficiently intensive sampling programme to permit an analysis of the variation in snail density parallel, as well as perpendicular, to the shoreline. However, the variability between sampling series was sometimes sub-

stantial (see July 25, 1968 and June 13, 1969, APPENDIX IX), and also, one sample collected on October 3, 1968, yielded many more snails than had any other sample on that or the two immediately preceeding sampling dates (APPENDIX IX). The extent of this variability emphasized the need for the replication of observations, and the samples were grouped, therefore, into only seven "distance classes": 0.0 to 1.0, 1.5 to 4.5, 5.0 to 8.0, 8.5 to 11.5, 12.0 to 15.0, 15.5 to 18.5 and 19.0 or more feet from shore. Replication had also been provided, of course, by replicate sampling series.

The first distance class, which was shorter than the others, was equivalent to the zone where wave action caused obvious modification of the bottom. Fine soil particles and detritus in this zone were floated into deeper water by even slight ripples, and the sand particles left behind formed a relatively unstable substratum. Snails and other macro-invertebrates were more or less absent from this distance class, except in sheltered locations or on calm days.

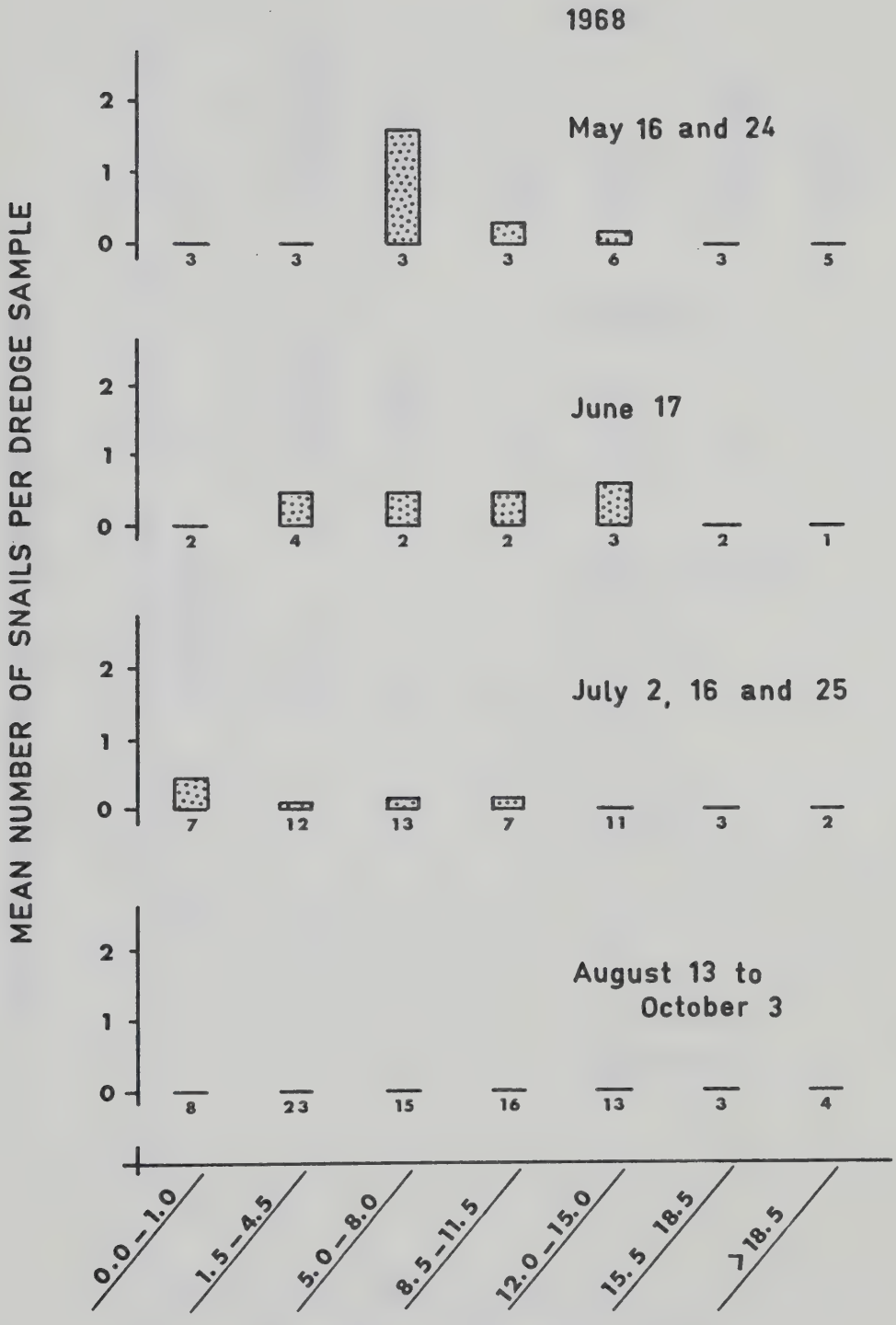
Because the slope of the bottom of the Clyde Pond was relatively constant over most of the zone sampled (Fig. 2), the pattern of the distribution of snails was virtually the same whether based upon water depth or distance from shore. Therefore, snail distribution was described only in terms of distance from shore.

Estimates of the density of *Helisoma trivolvis* were calculated for each distance class as the mean number of specimens recovered per dredge sample. Separate calculations were made for adult (Fig. 8) and juvenile (Fig. 9) snails, and the latter were further subdivided into five size classes. The first size class contained specimens less than 2.0 mm in diameter and those with broken shells. The limits of the remaining size classes were 2.0 to 4.9, 5 to 7.9, 8 to 10.9, and more than 10.9 mm.

The densities of empty juvenile shells (Fig. 9) were calculated similarly, except that the size class containing small and broken specimens included those under 5.0 mm in diameter instead of those under 2.0 mm. The 2.0 to 4.9 mm class was not applicable to the empty shells because at this size they were so fragile or weakened by erosion that relatively few were recovered intact.

In statistically analyzing the effects on the density of adult snails of sampling date, distance from shore and the interaction between these two factors, the sampling dates May, June, July, August and the composite of September and October were recognized. The distance classes considered were 1.5 to 4.5, 5.0 to 8.0, 8.5 to 11.5 and 12.0 to 15.0 feet from shore. The 0.0 to 1.0 ft distance class was excluded because, as previously noted (p.35), it encompassed a habitat which was used

Figure 8. Estimates of the density of adult *Helisoma trivolvis* in Clyde Pond during 1968 and 1969. The numerals shown indicate the number of dredge samples collected in each distance class.


1968
May 16 and 24
June 17
July 2, 16 and 25
August 13 to
October 3
MEAN NUMBER OF SNAILS PER DREDGE SAMPLE
0
1
2
3 3 3 3 6 3 5
2 4 2 2 3 2 1
7 12 13 7 11 3 2
8 23 15 16 13 3 4
0.0 – 1.0
1.5 – 4.5
5.0 – 8.0
8.5 – 11.5
12.0 – 15.0
15.5 18.5
> 18.5
FEET FROM SHORE

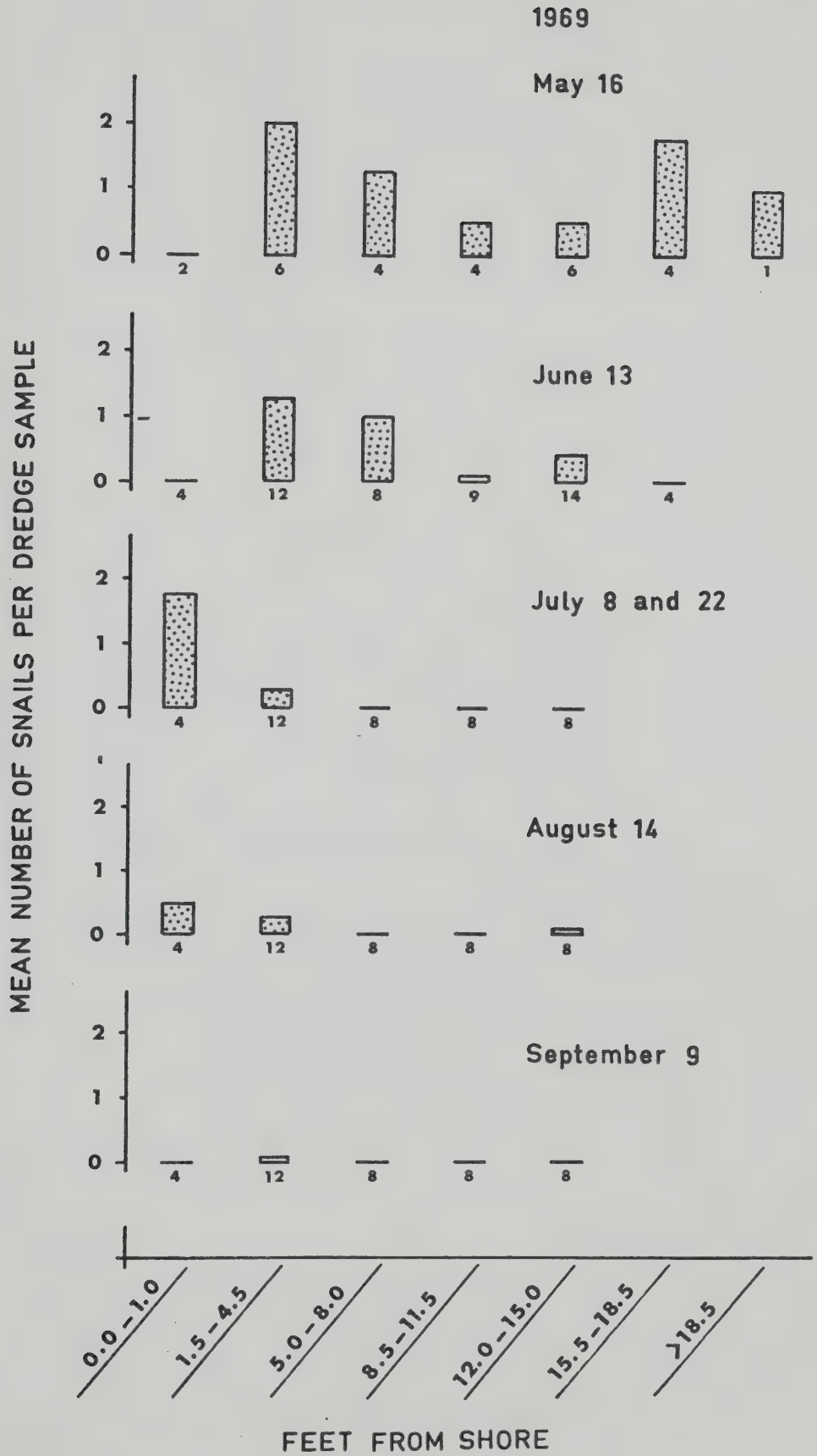
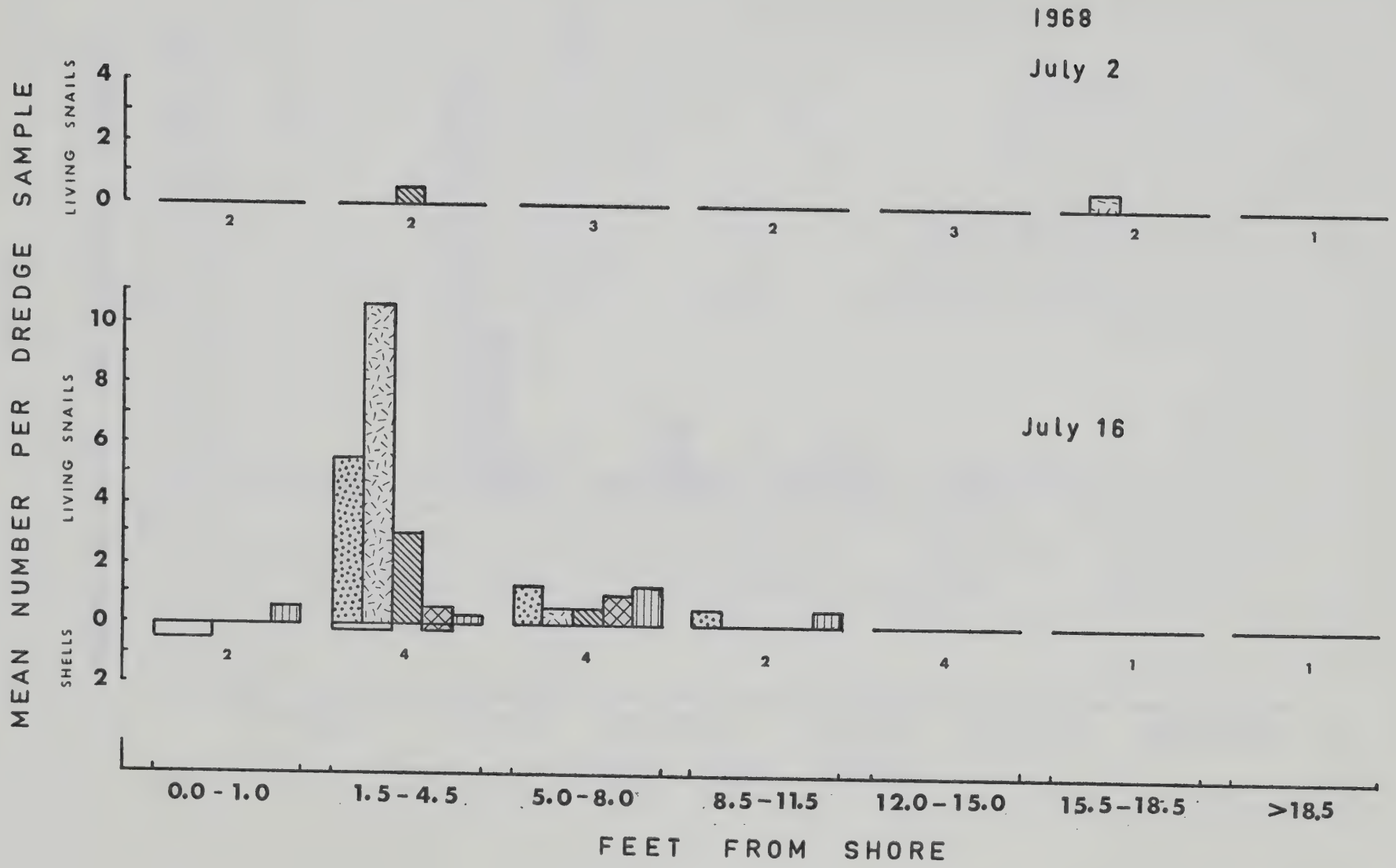
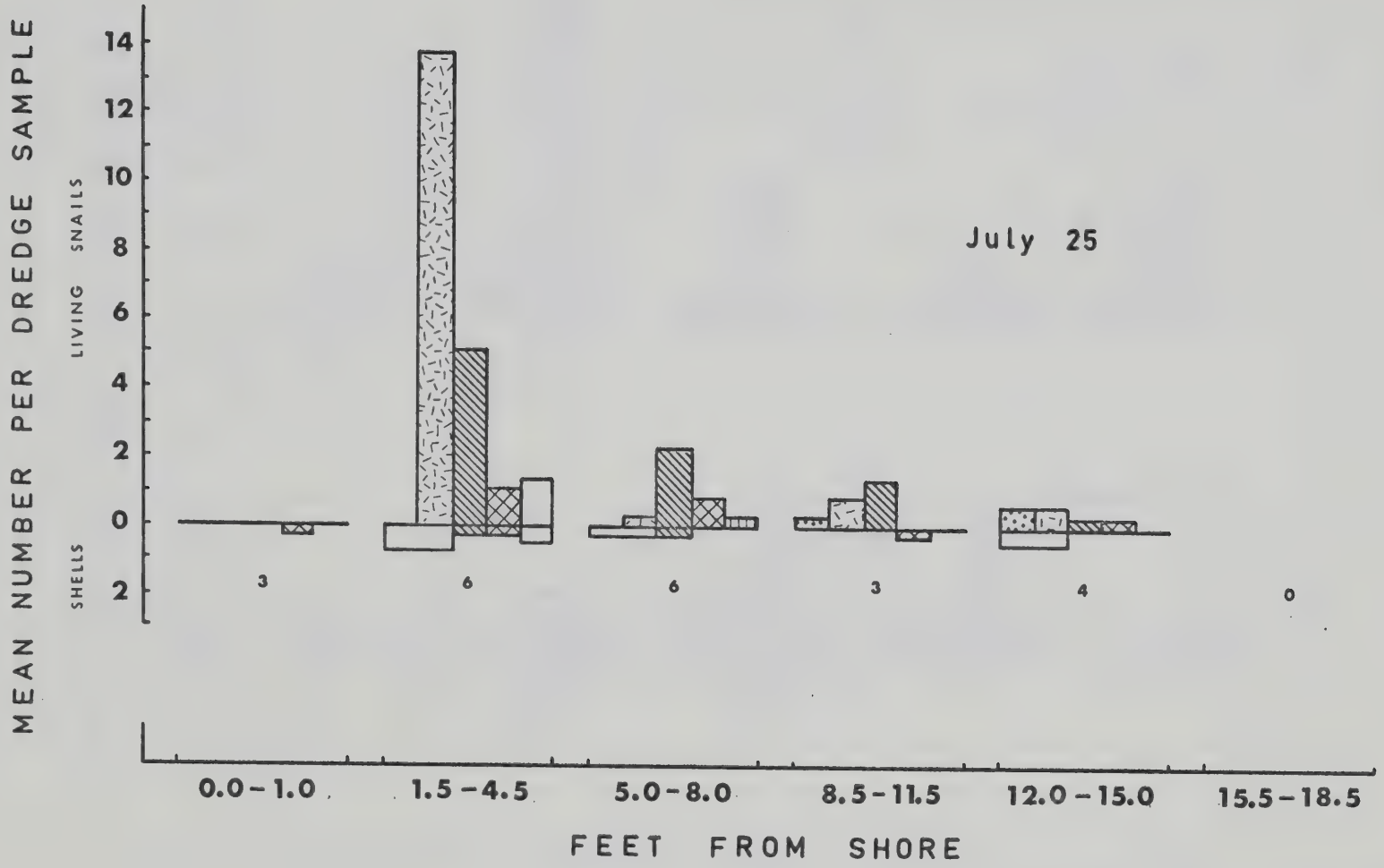
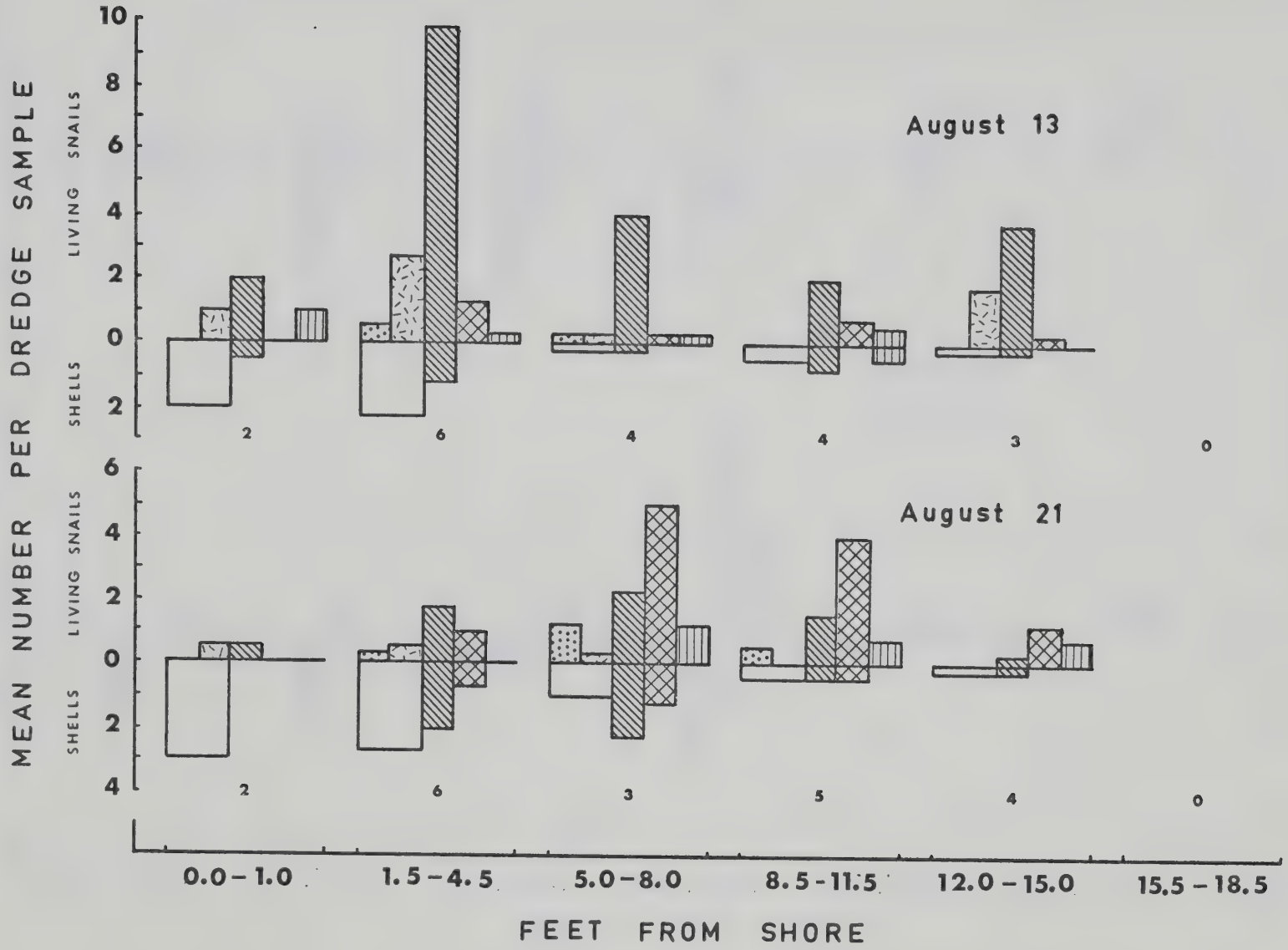

1969
May 16
June 13
July 8 and 22
August 14
September 9
MEAN NUMBER OF SNAILS PER DREDGE SAMPLE
0
1
2
2 6 4 4 6 4 1
4 12 8 9 14 4
4 12 8 8 8
4 12 8 8 8
4 12 8 8 8
0.0–1.0
1.5–4.5
5.0–8.0
8.5–11.5
12.0–15.0
15.5–18.5
>18.5
FEET FROM SHORE

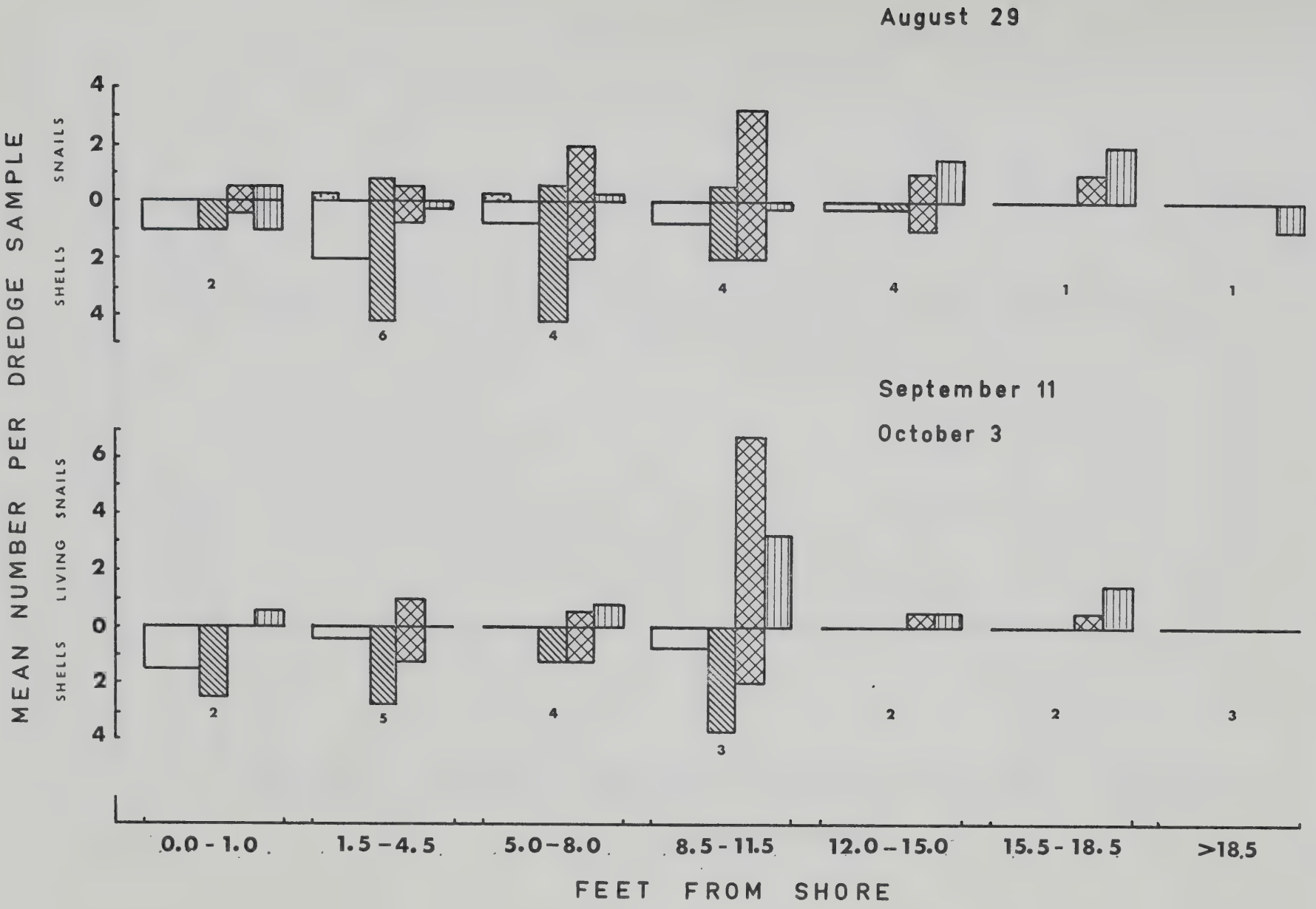
Figure 9. Estimates of the density of juvenile *Helisoma trivolvis* (living snails and empty shells) in Clyde Pond in 1968 and 1969. The numerals shown indicate the number of dredge samples collected in each distance class.

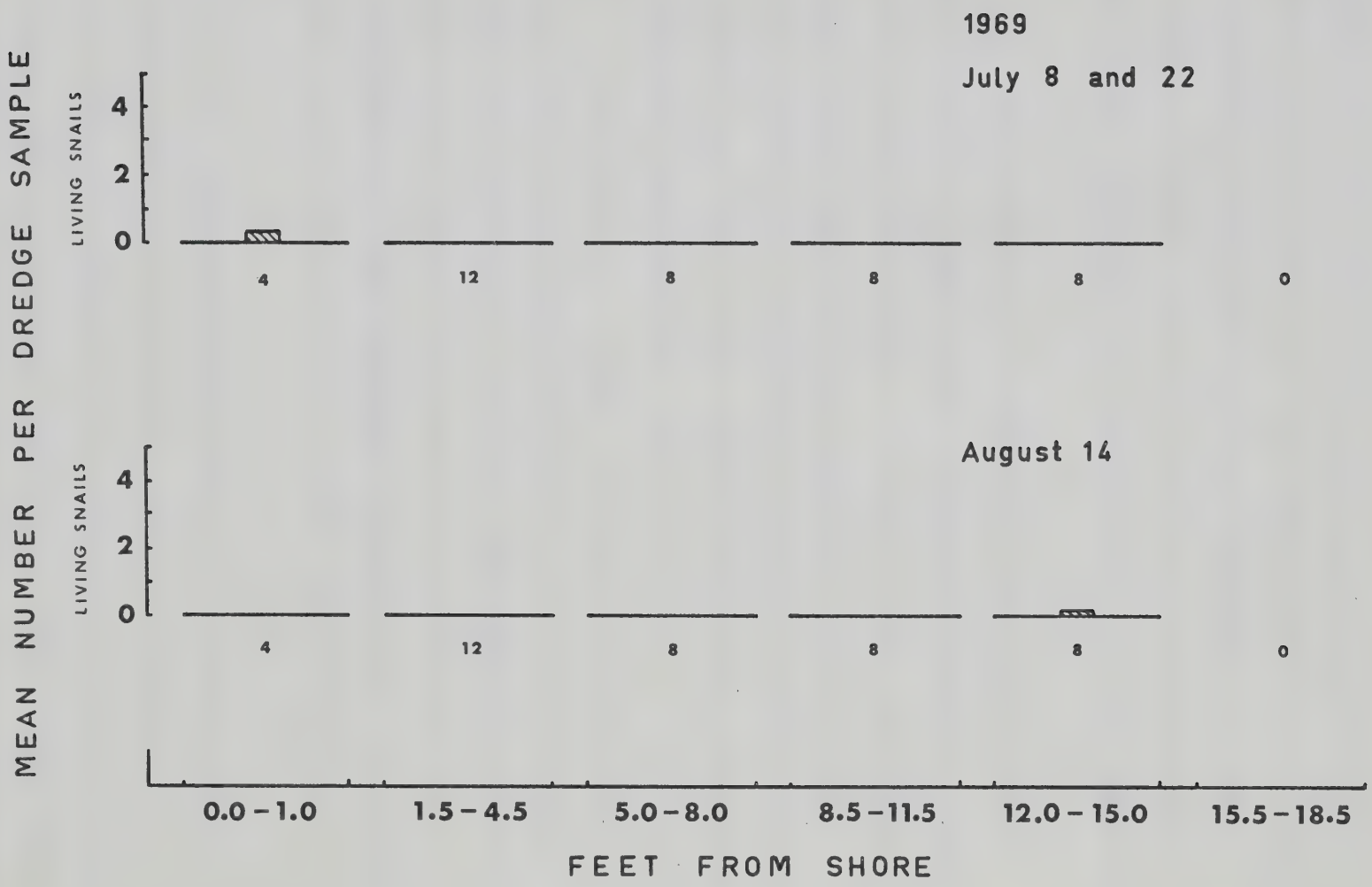
Diameter Class
<2.0 mm, or broken
<5.0 mm, or broken
2.0 - 4.9 mm
5.0 - 7.9 mm
8.0 - 10.9 mm
>10.9 mm


1968
July 2
July 16
MEAN NUMBER PER DREDGE SAMPLE
LIVING SNAILS
SHELLS
LIVING SNAILS
4
2
0
10
8
6
4
2
0
2
2
3
2
3
2
1
2
4
4
2
4
1
1
0.0 - 1.0
1.5 - 4.5
5.0 - 8.0
8.5 - 11.5
12.0 - 15.0
15.5 - 18.5
>18.5
FEET FROM SHORE


MEAN NUMBER PER DREDGE SAMPLE
SHELLS
LIVING SNAILS
14
12
10
8
6
4
2
0
2
July 25
3
6
6
3
4
0
0.0 – 1.0
1.5 – 4.5
5.0 – 8.0
8.5 – 11.5
12.0 – 15.0
15.5 – 18.5
FEET FROM SHORE


MEAN NUMBER PER DREDGE SAMPLE
SHELLS
LIVING SNAILS
10
8
6
4
2
0
2
August 13
2
6
4
4
3
0
6
4
2
0
2
4
August 21
2
6
3
5
4
0
0.0 – 1.0
1.5 – 4.5
5.0 – 8.0
8.5 – 11.5
12.0 – 15.0
15.5 – 18.5
FEET FROM SHORE


August 29
September 11
October 3
MEAN NUMBER PER DREDGE SAMPLE
SHELLS SNAILS
SHELLS LIVING SNAILS
4
2
0
2
4
6
2
6
4
4
4
1
1
2
5
4
3
2
2
3
0.0 - 1.0
1.5 - 4.5
5.0 - 8.0
8.5 - 11.5
12.0 - 15.0
15.5 - 18.5
>18.5
FEET FROM SHORE


1969
July 8 and 22
LIVING SNAILS
4
2
0
4
12
8
8
8
0
August 14
LIVING SNAILS
4
2
0
4
12
8
8
8
0
MEAN NUMBER PER DREDGE SAMPLE
0.0 – 1.0
1.5 – 4.5
5.0 – 8.0
8.5 – 11.5
12.0 – 15.0
15.5 – 18.5
FEET FROM SHORE

by snails only when wave action was negligible. To have included the data from this area merely would have burdened the statistical tests with a larger experimental error. The distance classes beyond 15 feet from shore were excluded because they were not represented at every sampling time.

As evidenced by significant declines in their density ($P_o < 0.01$), adult *Helisoma trivolvis* suffered high mortality during the summers of both 1968 and 1969 (Fig. 8), but this mortality was not complete, even in 1968, since in August 1968 a few adults were observed in the pond, and 10 per cent of the adults collected in 1969 were more than one year old (Fig. 7).

The density of adult *Helisoma trivolvis* was significantly greater ($P_o < 0.01$) in May 1969 than in May 1968 (Fig. 8); therefore, the snail population had been expanding during 1968. Both general observations, and the data obtained from dredging, indicated that in the fall also the density of adults was greater in 1969 than in 1968.

No significant differences in the density of adult snails were detected among distance classes ($P_o > 0.05$), but the effect of the interaction between time and distance was significant ($P_o < 0.01$). Thus, while none of the distance classes were consistently the most heavily populated by adults there had been an increasing tendency,

from May to August, for these snails to be located near the shore (Fig. 8). The data for September and October suggested, though very weakly because of the low number of specimens recovered, that this trend was reversed in the fall.

Thick mats of *Myriophyllum exalbescens* were present along parts of the shoreline of Clyde Pond after midsummer in both years, and these tended to dissipate waves before they reached the shore. Mature *Helisoma trivolvis* were often seen very near the shore in such protected locations (Fig. 8), but they were found here comparatively rarely after the last week of August. This was considered to be further evidence of an autumn migration into deeper water.

Another possibly related observation was that *Helisoma trivolvis* became more or less inactive in Clyde Pond after about the end of August. Specimens were typically found withdrawn into their shells, along with a small amount of mud, and lying on the pond bottom. Also, when brought into the laboratory they exhibited little activity for at least several weeks.

In 1968, juvenile snails were first recovered on July 2, but they were not prominent in dredge samples until July 16 (Fig. 9). Apparently they had been too small before this time to be distinguished from the other material in the samples. The differences in the density

of juvenile snails among sampling dates (July 16, July 25, August 13, August 21, August 29, and the composite of September and October 1968) were statistically significant ($P_o < 0.01$). The same distance classes included in the analysis of the density of adults were also considered here. The differences revealed by the above general analysis were located by statistically testing pairs of consecutive sampling dates. No significant differences in density were detected among July 16, July 25, and August 13 ($P_o > 0.05$), but, significant declines were detected between August 13 and August 21 ($P_o < 0.05$) and between August 21 and August 29 ($P_o < 0.01$). There was no significant change in density from August 29 to September - October ($P_o > 0.05$).

In 1969, virtually no juvenile *Helisoma trivolvis* were recovered from dredge samples (Fig. 9), and very few were obtained by any means.

To summarize the changes in the sizes of both mature and juvenile populations, density estimates were translated into abundance indexes for each sampling date. For each distance class, the mean number of snails recovered per dredge sample was multiplied by the number of six-inch-wide dredge samples that would have exactly filled that class. The several products thus obtained for each collection date were added together, and the total became the "Abundance Index" (Table 3).

Table 3. Abundance Indices for juvenile and adult *Helisoma trivolvis* in Clyde Pond, from May 1968 to September 1969.

	Date	Abundance Index Juveniles	Adults
1968	May 16	0.0	15.2
	May 24		
	June 17	0.0	15.2
	July 2	7.0	
	July 16	177.8	3.5
	July 25	197.1	
	August 13	209.2	
	August 21	160.9	0.0*
	August 29	97.6	
	Sept. 11	107.8	0.0*
	Oct. 3		
1969	May 16	0.0	44.0
	June 13	0.0	19.5
	July 8	0.5	5.2
	July 22		
	August 14	0.8	3.6
	Sept. 9	0.0	0.6

* Underestimates: see 1969 collections, Figure 7.

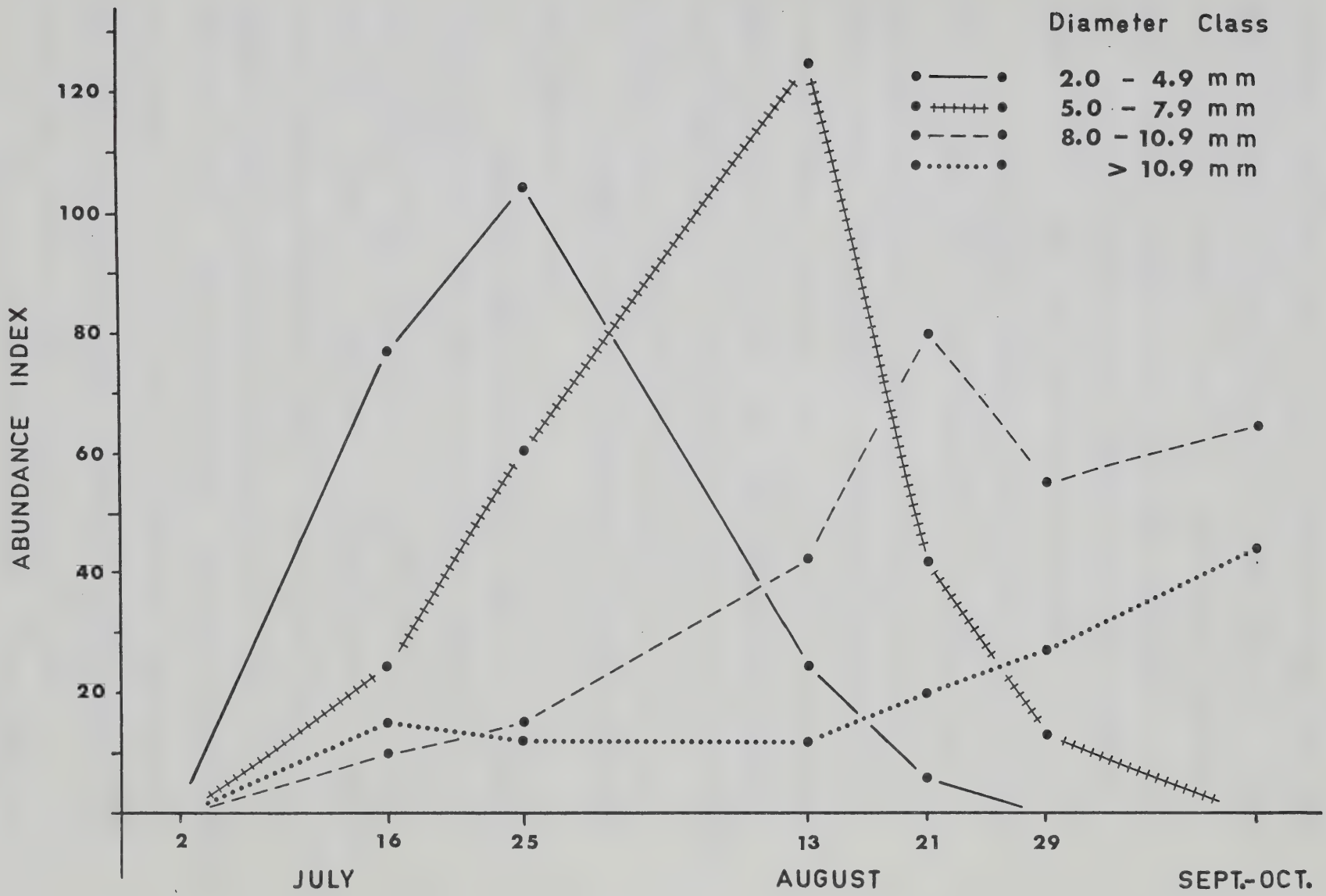
The Abundance Index was approximately equivalent to the total number of specimens present in the six-inch-wide transect running perpendicular to the shoreline, from the water's edge to about 20 ft from shore (total area about 10 sq ft). Since the bulk of the snail population occurred within this zone (Fig. 8 and 9), changes in the Abundance Index were considered applicable to the whole population.

The significance of a difference between Abundance Index values may best be judged by the significance of the difference between corresponding density estimates.

When the Abundance Index for juvenile snails in 1968 was partitioned according to size classes (see Fig. 9), it was found that, while the number of snails between 8.0 and 10.9 mm in diameter had increased markedly from July 16 to August 21, the number of snails over 10.9 mm in diameter had remained relatively constant (Fig. 10). Since there had not been simply a disproportionately high mortality rate among the larger snails (Fig. 9), it was concluded that the growth rate of juvenile *Helisoma trivolvis* had declined to almost zero after they entered the 8.0 - 10.9 mm size class. Possibly general growth was halted because of physiological demands associated with preparation for the ensuing spawning season (pp.69 and 70).

The densities of the empty shells of juvenile

Figure 10. Changes in the Abundance Index for each size class of living juvenile *Helisoma trivolvis* during 1968.


Diameter Class
2.0 - 4.9 mm
5.0 - 7.9 mm
8.0 - 10.9 mm
> 10.9 mm
ABUNDANCE INDEX
120
100
80
60
40
20
2
16
25
13
21
29
JULY
AUGUST
SEPT.-OCT.

Helisoma trivolvis (Fig. 9) were significantly different ($P_o < 0.01$) among collection dates in 1968 (July 25, August 13, August 21, August 29 and the composite of September and October). Since empty shells were numerous within a few inches of the shoreline, samples from all distance classes to 15 feet from shore were considered.

Since this analysis could not locate the significant differences it had detected, the differences between paired consecutive sampling times were also tested statistically. Significant increases in density were revealed between August 13 and 21 ($P_o < 0.05$) and between August 21 and 29 ($P_o < 0.05$), but the differences between July 25 and August 13 and between August 29 and September-October, were not significant ($P_o > 0.05$).

No empty shells of juvenile *Helisoma trivolvis* were obtained in 1969.

Both the distance from shore, and the interaction between distance from shore and time of sampling, had significant effects ($P_o < 0.01$) on the density of *Helisoma trivolvis* (Fig. 9). That is, the distribution of juvenile snails was correlated with the distance from shore, but the nature of this correlation changed progressively with the advancing date. More specifically, the snails had remained concentrated in the 1.5 to 4.5 ft distance class through July, but in August, and particularly in mid-August, they began to be found further and further from shore.

Concurrently with this movement, the snails be-

came less and less concentrated within particular distance classes, until finally, in September and October, the probability that the observed distribution of snails had occurred by chance alone, was approximately 0.40.

This distribution pattern probably was maintained throughout the winter, since on May 16, 1969 there was no significant difference ($P_o > 0.05$) in density among distance classes (Fig. 8). In this analysis, all distance classes between 1.5 to 18.5 feet from shore were considered.

In the fall of 1968, even though there had been no real differences in juvenile snail density among distance classes, there was a wide range of variability among samples (APPENDIX IX). On October 3, one sample had yielded 27 snails, while no other sample held more than six, and the mean number recovered for all other samples was about one. This uncommonly large sample may have resulted from a tendency for *Helisoma trivolvis* to occur in aggregations in the fall. Since only one such sample was collected, the possibility existed that such clumping was atypical of the whole population, but if it was typical, such behavior could function in bringing partners together for mating.

Unfortunately, copulation of *Helisoma trivolvis* was never observed in Clyde Pond, but if this species copulates in the early spring as does *Physa gyrina* (DeWitt 1954a), to become aggregated just before and during winter

would seem advantageous. Unlike *Physa gyrina*, *Helisoma trivolvis* was very slow moving when water temperatures were below about 10°C. Thus the combination of clumping and a tendency toward inactivity in the autumn (p.40) could greatly facilitate the search for mating partners in the spring. Copulation is probably of critical importance to efficient reproduction in *Helisoma trivolvis* since DeWitt and Sloan (1959) have found the Planorbidae to be poorly adapted for self fertilization.

The effect on the density of juvenile *Helisoma trivolvis* of the interaction between distance from shore and shell diameter, was significant ($P_o < 0.01$). All specimens over 2.0 mm in diameter were included in this analysis. It was concluded, by reference to Fig. 9, that snails in the 2.0 to 4.9 mm size class were abundant only in the 1.5 to 4.5 ft distance class, while progressively larger snails were most numerous at progressively greater distances from shore.

Since the effect of this interaction between distance from shore and diameter, and that of the previously mentioned interaction, between distance from shore and sampling time (p.45), were somewhat parallel, there arose the possibility that shell diameter and sampling date were merely two different expressions of the effect of the passage of time. This ambiguity could not be resolved by the data available.

Twenty-one egg masses were deposited in the tall aquarium at a mean depth of 36 inches. All the eggs hatched on the ninth and tenth days after oviposition, and after hatching was completed, 290 snails were counted. Their distribution in the aquarium was just the opposite of the distribution of egg masses; 30 per cent were found within one inch, and 50 per cent within one foot of the water's surface. Obviously a relatively rapid upward migration had occurred.

One day later, about 15 per cent of the snails were found within an inch, and 40 per cent within a foot of the surface. There also seemed to be a slight concentration of snails near the bottom of the aquarium, apparently as a result of snails having lost their attachment at the surface of the water, after which they settled passively to the bottom.

On the third day of observations, the pattern of distribution had changed completely and the new pattern was maintained until the experiment was terminated two and a half months later. During this period relatively few of the snails were observed at the water's surface or on the walls of the aquarium, and those that were showed no obvious depth preference. The majority of the snails were now on the bottom of the aquarium, hidden in a thin layer of debris. The snails falling to the bottom of the aquarium apparently found an attractive environment, and

either the tendency to migrate to the water's surface had been lost by this time, or this tendency was weaker than that to remain in the debris.

Possibly the debris contained a source of food. Bovbjerg (1965) found that *Stagnicola reflexa* moved more or less randomly with respect to food until a suitable source was discovered. Movement then ceased as feeding began, and over a period of time animals became aggregated at the food source.

Reproduction

Helisoma trivolvis performed a more or less stereotyped series of activities in depositing its egg masses. Having selected the spawning site, a snail typically spent up to 30 minutes in scraping clean, with the radula, an area of the substrate about 2 cm in diameter. Radular movements then ceased, and they were not resumed until after the egg mass had been deposited and abandoned. The snail then positioned itself near the centre of the cleaned area, and retracted its head and the anterior half of its foot into its shell. In a minute or less the egg mass appeared beneath the anterior of the snail's foot, and it was immediately pressed against the cleaned substrate by the re-extension of the foot and head. The egg mass, consisting of many eggs in an amorphous gelatinous matrix, was flattened and became

nearly circular in outline. The snail spent the following 30 to 90 minutes alternately resting with its foot covering the egg mass, and travelling back and forth across it. During this period the egg mass seemed to contract slightly as it became affixed to the substrate. Its attachment was particularly firm near its perimeter.

The snail finally abandoned the egg mass, and within a few minutes began normal feeding activity.

Specimens of *Helisoma trivolvis* of all ages from one to five years old were brought from Clyde Pond into the laboratory in May 1969. Some of these snails were maintained in isolation from one another, and within a few days representatives of each age group had produced at least one egg mass. The only specimens which failed to produce egg masses had been damaged in collection or were heavily infected with trematode rediae (p.80).

Hyman (1968:613) concluded, in reviewing the literature, that most basommatophorans die after one spawning. It was apparent that either *Helisoma trivolvis* is atypical of its order, or else the literature contains errors in this regard.

The relationship between the size of the snail and the number of eggs per egg mass was not specifically investigated in *Helisoma trivolvis*. However, there seemed to be general agreement with DeWit's (1955) observations on *Physa fontinalis* that the size of egg masses was linear-

ly correlated with the size of the shell. DeWitt (1954b) has shown also that the shell height in *Physa gyrina* was linearly correlated with total egg production.

The 102 usable egg masses collected in 1968 from natural substrata in Clyde Pond contained from 11 to 68 eggs per egg mass. A mean of 37 eggs per egg mass was calculated, and there was no difference among the means for May, June and July. There was also no difference between the means for egg masses from natural and Plexiglas substrata.

Of the 95 egg masses collected by dredge sampling in 1968, 78 per cent had been deposited on dead, but as yet undecayed, stems of aquatic plants, primarily *Myriophyllum exalbescens*. Only 4 per cent were found on living *Myriophyllum exalbescens*, although it was available in abundance, but 18 per cent were attached to the shells of living *Helisoma trivolvis*. Egg masses were never found on empty snail shells. Stones from adjacent farmlands had been dumped into the pond at several locations, and since these areas could not be sampled with an Ekman dredge, the extent to which stones were acceptable as spawning substrata was evaluated merely by inspection. Stones approximately four or five inches in diameter commonly carried several egg masses, and it was estimated that, where available, stones were used to about the same degree as dead plant stems.

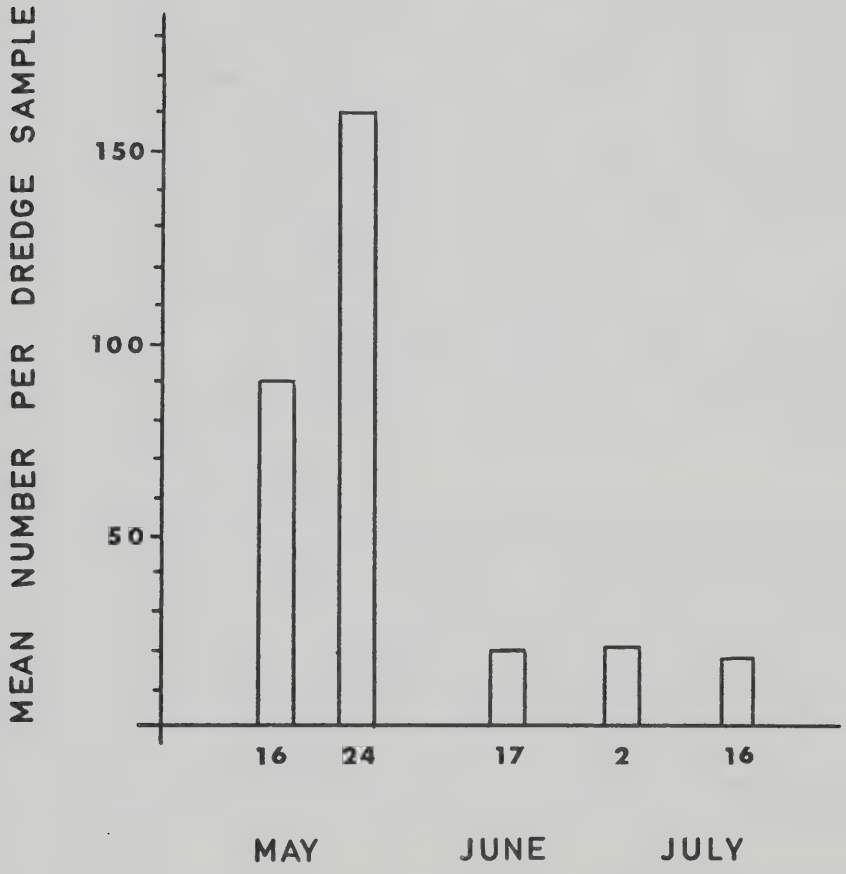
The egg masses found on vegetation were in dredge samples collected between 3 and 9 feet from shore (water depths were between 9 and 24 inches). Eggs found on rock and Plexiglas substrata, however, were taken from water between 2 and 54 inches deep, and it seemed likely that the location of the spawning sites was influenced more by the availability of an acceptable substratum than by the depth of the water.

In 1968, the onset of spawning was not recorded in Clyde Pond because egg masses of *Helisoma trivolvis* were found on the first sampling date (May 16). The peak of spawning apparently occurred near the end of May, but some oviposition continued into early July (Fig. 11).

Newly deposited egg masses were also obtained from Clyde Pond in 1968, through 24 or 48 hour trials of the acceptability of Plexiglas as a substratum for spawning. The relative numbers of egg masses deposited on the Plexiglas indicated that the rate of spawning of *Helisoma trivolvis* was relatively high on May 29, but that it had declined 60 per cent by June 12, and 85 per cent by July 16.

In 1969, a relatively early spring was experienced, and in Clyde Pond *Helisoma trivolvis* began spawning on natural substrata between May 1 and May 5. Egg masses appeared on the Plexiglas substrates at the same time (APPENDIX X), indicating a ready acceptance of them by the snails.

Figure 11. The mean number of eggs of *Helisoma trivolvis* recovered per dredge sample for sampling dates in 1968 (all samples from 1.5 to 15.0 feet from shore are included).


MEAN NUMBER PER DREDGE SAMPLE
150
100
50
16
24
17
2
16
MAY
JUNE
JULY

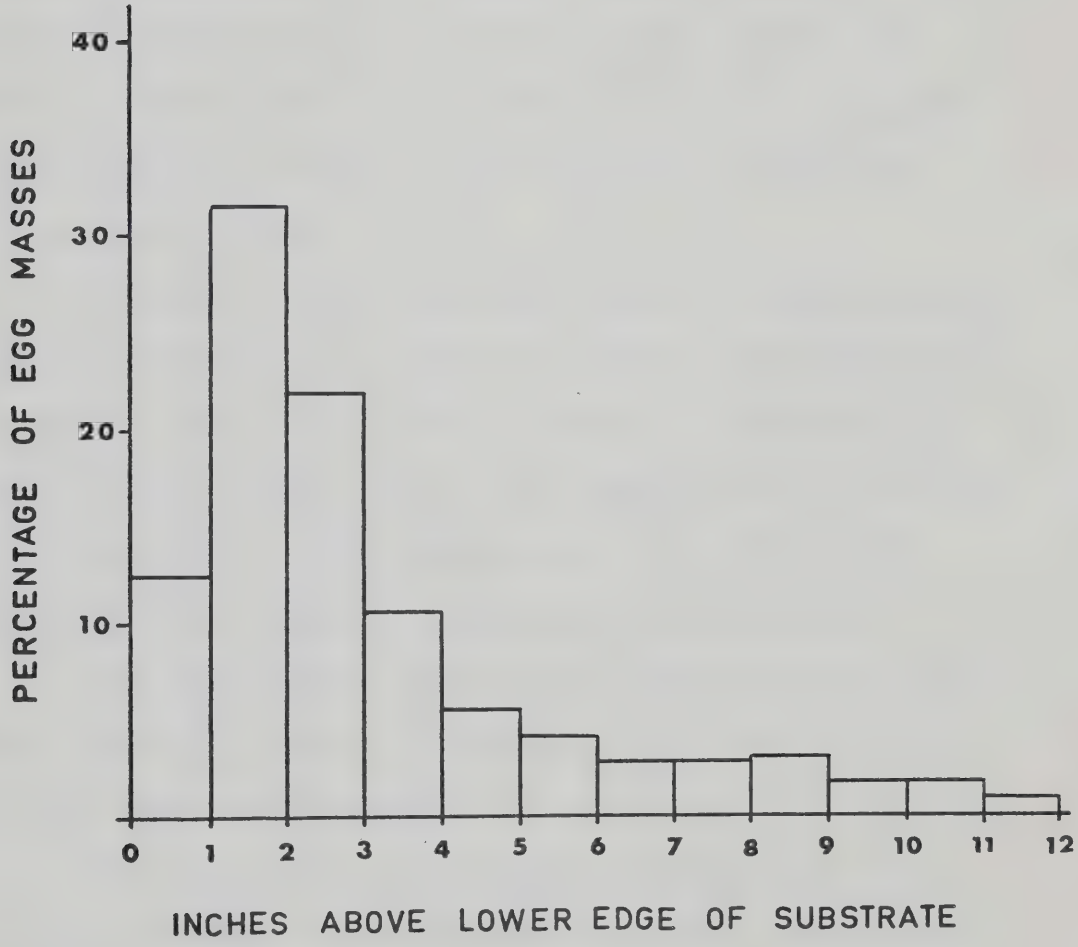
Most of the egg masses deposited on the Plexiglas were from *Helisoma trivolvis*, but those of *Lymnaea stagnalis* and *Physa gyrina* also appeared occasionally.

Helisoma trivolvis egg masses were concentrated near the lower edges of the Plexiglas substrates (Fig. 12), though they were usually placed somewhat above the surface of the bottom mud. The depth to which substrates sank into the bottom was evidenced by traces of mud clinging to the Plexiglas, and this distance was generally between 1/2 and 3/4 of an inch. Egg masses on the inner surfaces of the substrate did not appear to be concentrated at any particular level. Because they were few and difficult to examine closely, egg masses on the inner surfaces of these substrates were ignored.

This pattern of distribution, plus the fact that 90 to 95 per cent of the egg masses were deposited on the outer surfaces of the substrates, was considered further evidence that gravid snails, began oviposition almost immediately after encountering an acceptable type of substratum.

In the horizontal plane, the distribution of egg masses on the Plexiglas substrates was not significantly different from a random distribution ($P_o > 0.05$). However, the variance/mean ratio was approximately 0.86, which implied there had been a tendency towards a uniform distribution. This may have been a reflection of the fact that egg masses

Figure 12. The vertical distribution of 1033 *Helisoma trivolvis* egg masses deposited on Plexiglas substrates in Clyde Pond in 1969.


PERCENTAGE OF EGG MASSES
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
INCHES ABOVE LOWER EDGE OF SUBSTRATE

never quite touched one another, even though up to six were occasionally deposited within one square inch.

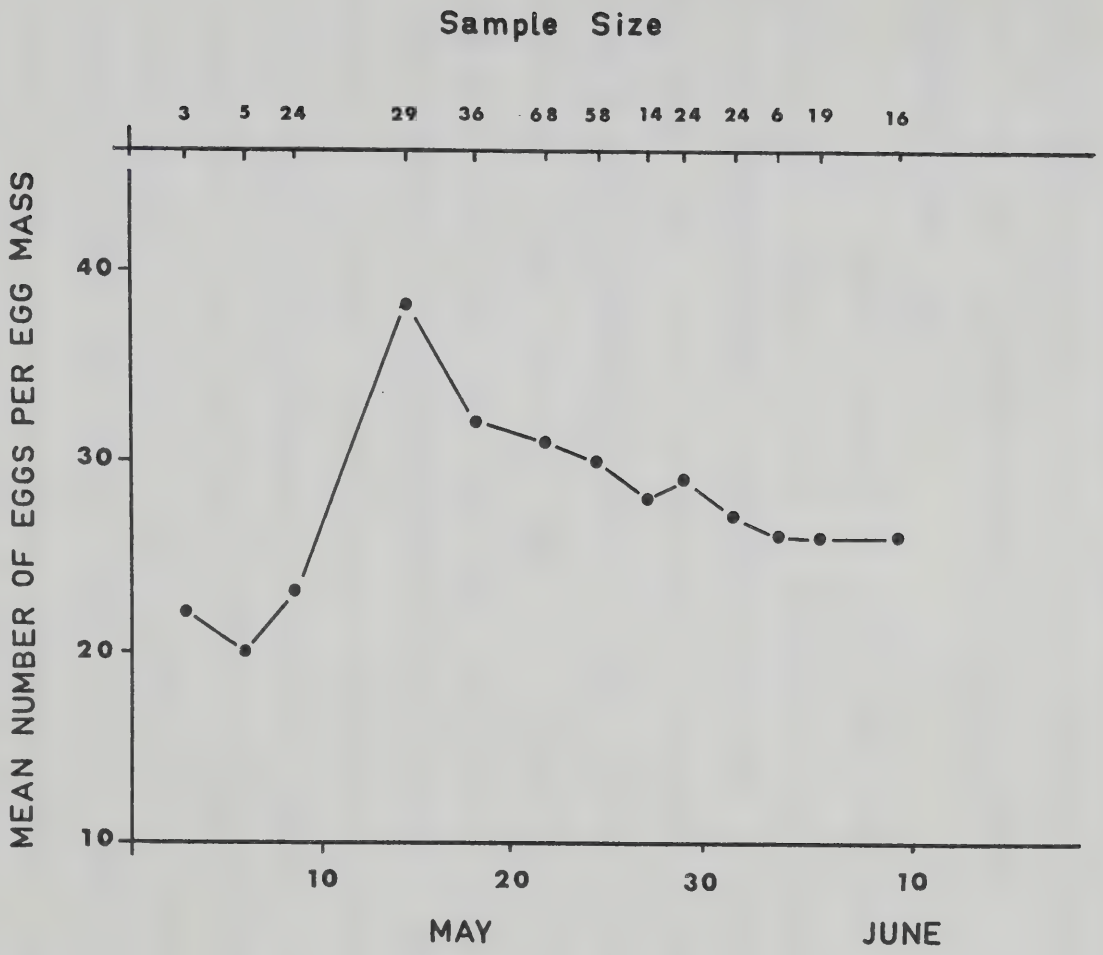
Between 5 and 10 per cent of the egg masses deposited on the substrates disappeared before they had hatched, but it was not learned whether these had been removed by predators or had simply become detached. The latter explanation seemed the most likely, since the missing egg masses were gone without trace, and only two partially damaged egg masses were observed during the entire spawning season.

Figure 13 shows the mean number of eggs recorded per egg mass of *Helisoma trivolvis* through the 1969 spawning season. The initial sharp increase, followed by a gradual decline to the end of the spawning season correspond with McCraw's (1952) observations on *Stagnicola palustris* brought into the laboratory in the spring.

The mean number of eggs per egg mass was significantly ($P_o < 0.05$) lower in 1969 than in 1968, but the reason for this was not clear.

To facilitate statistical analyses, the 12 Plexiglas substrates were grouped, by fours, into three categories of distance from shore. The ranges of distance from shore for these categories were initially 1.0 to 5.5, 7.5 to 11.5 and 13.0 to 17.5 feet, and their mean distances from shore were about 3, 9 and 15 feet. During the spawning season, declining water levels (APPENDIX II) caused

Figure 13. Changes in the mean number of eggs per egg mass of *Helisoma trivolvis* during the 1969 spawning season. The egg masses had been deposited on Plexiglas substrates in Clyde Pond.

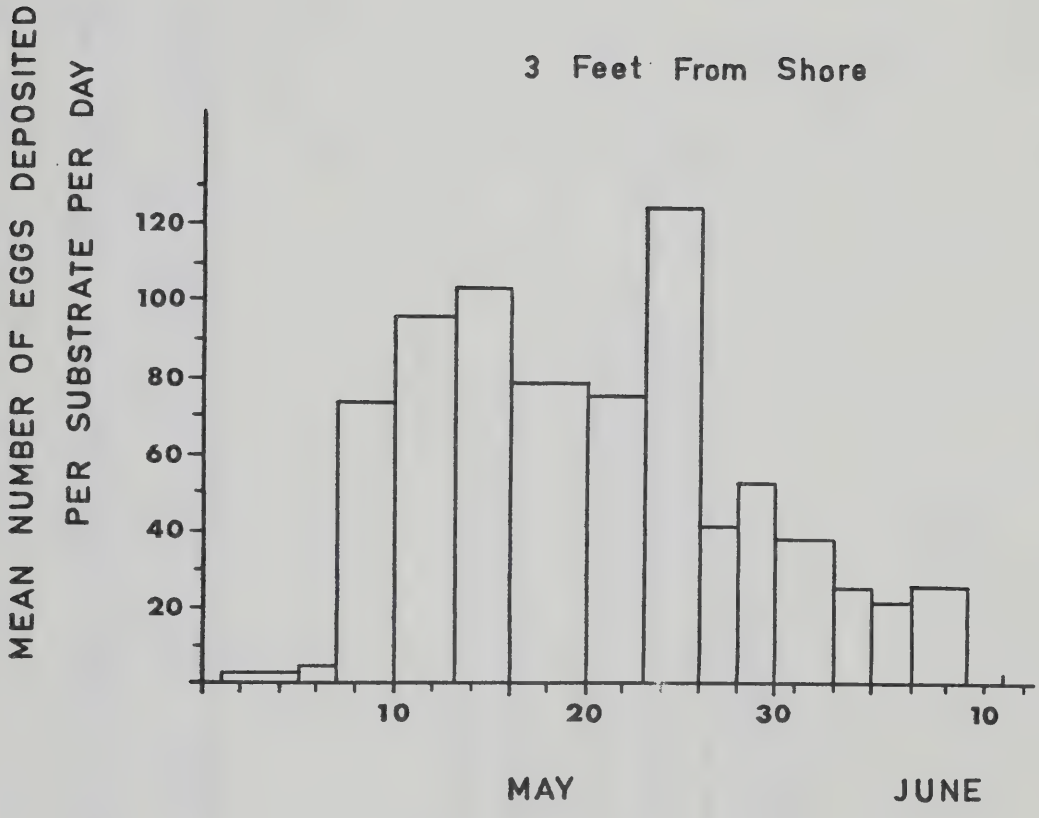

Sample Size
3 5 24 29 36 68 58 14 24 24 6 19 16
MEAN NUMBER OF EGGS PER EGG MASS
40
30
20
10
10 20 30 10
MAY
JUNE

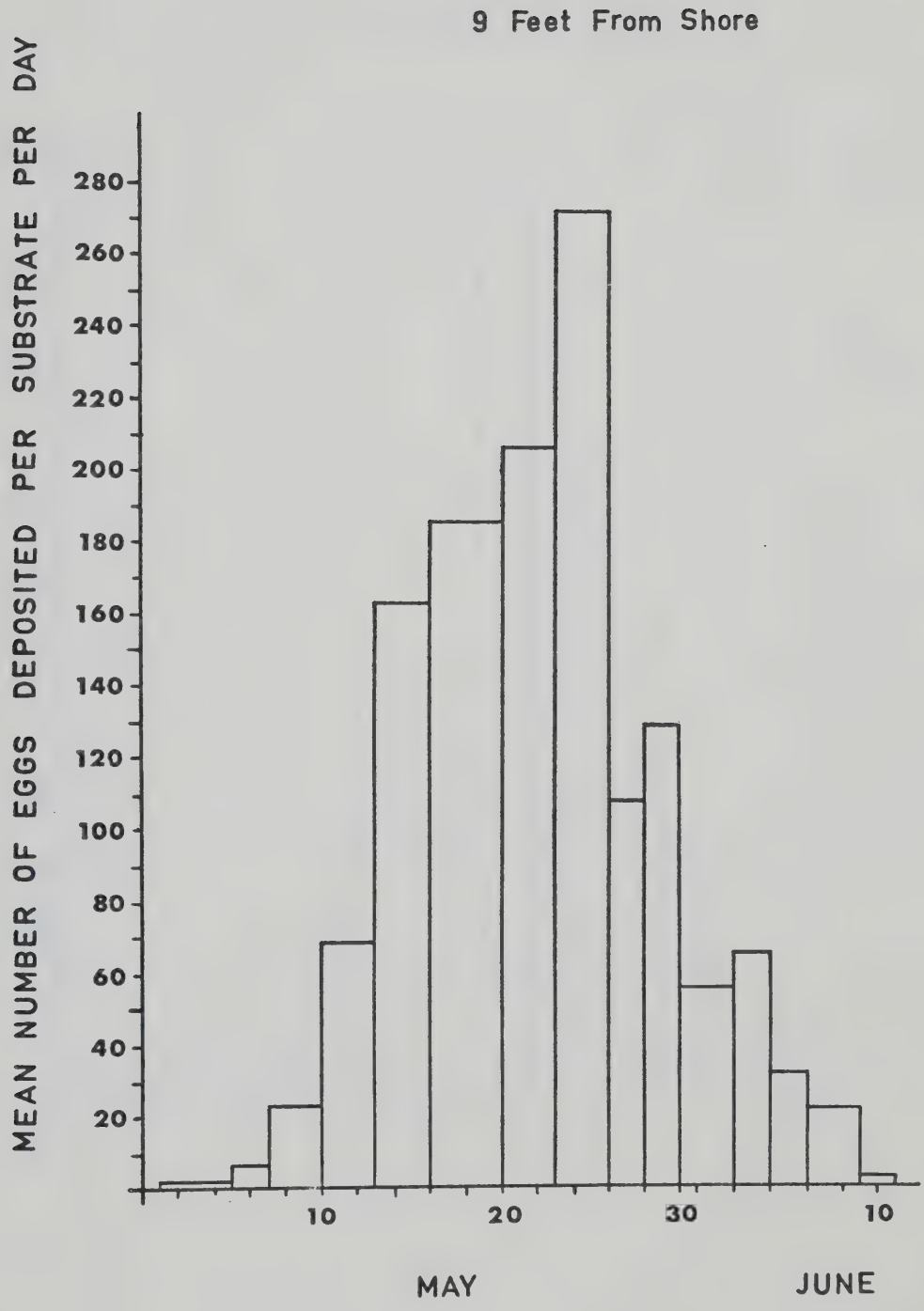
the shoreline to retreat about 1.5 feet and these distances were therefore decreased accordingly. This also resulted in substrate number 1, the substrate nearest the shoreline, becoming unavailable to the snails after about May 15.

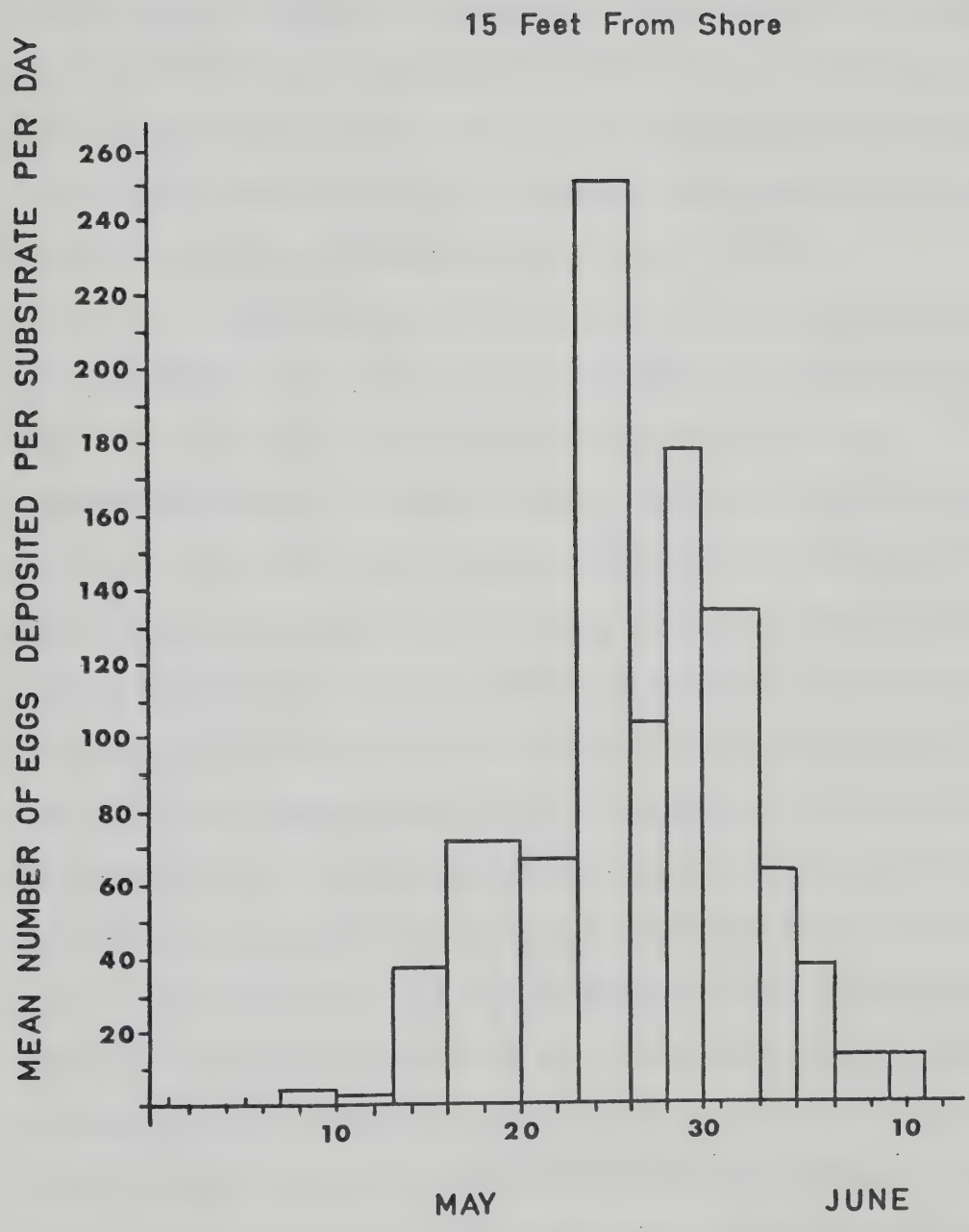
The mean number of *Helisoma trivolvis* eggs deposited per substrate per day in each distance category (Fig. 14), was calculated from the data recorded in APPENDIX X and Fig. 13.

It became clearer in 1969 (Fig. 14) than it had been in 1968 (Fig. 11) that in *Helisoma trivolvis* spawning was fundamentally a springtime activity of finite duration. The snails appeared to be prepared, at the beginning of the spawning season, to lay a more or less predetermined total number of eggs, and ceased spawning for the year once these eggs had been deposited. These findings when combined with the knowledge that the snails were capable of spawning repeatedly in subsequent springs (p.50), was yet another contradiction of several reports in the literature. It has been both stated and implied, for *Lymnaea stagnalis* (Noland and Carriker, 1946), *Lymnaea columella* (DeWitt and Sloan, 1958), *Lymnaea humilis* (McCraw, 1961), *Lymnaea peregra* (Hunter, 1961a), *Lymnaea emarginata* (Howard and Walden, 1965), *Stagnicola palustris* (Eisenberg, 1966), *Physa gyrina* (DeWitt, 1955), *Physa fontinalis* (De Wit, 1955; Duncan, 1959; Hunter, 1961a), and *Physa spp.* (Howard and Walden, 1965), that once spawn-

Figure 14. Rates of spawning by *Helisoma trivolvis*, on Plexiglas substrates, at three distances from shore in Clyde Pond, in 1969.


3 Feet From Shore
MEAN NUMBER OF EGGS DEPOSITED PER SUBSTRATE PER DAY
120
100
80
60
40
20
10
20
30
10
MAY
JUNE


9 Feet From Shore
MEAN NUMBER OF EGGS DEPOSITED PER SUBSTRATE PER DAY
280
260
240
220
200
180
160
140
120
100
80
60
40
20
10
20
30
10
MAY
JUNE


15 Feet From Shore
MEAN NUMBER OF EGGS DEPOSITED PER SUBSTRATE PER DAY
260
240
220
200
180
160
140
120
100
80
60
40
20
10
20
30
10
MAY
JUNE

ing is initiated it continues unabated until the snail becomes senescent or dies. Agersborg (1932) reported that *Physa gyrina* spawned throughout the year in an artificially warmed ditch in Illinois. De Witt (1955; 1967) concluded that regardless of the season or photoperiod, oviposition would only be interrupted if water temperatures dropped below a certain critical level (about 10°C).

Helisoma trivolvis is not among the species listed above, and there is a possibility that its reproductive behaviour is different from these other basommatophorans. Nevertheless, one can hardly overlook the fact that all the studies cited either failed, in considering populations, to take stock of the variation among individuals, or failed to determine whether the conditions under which the snails had lived before the investigations began were of any importance. The fact that a population of snails produced egg masses continuously should not have been considered evidence that individual snails had done so. It could equally well have occurred through asynchronous spawning of individuals having relatively short reproductive periods. It may be significant that Jenner (1951), who demonstrated that *Stagnicola palustris* did not spawn in the laboratory under photoperiods of less than 13.5 hours, had obtained his specimens from the field in the late autumn, while De Witt (1967), using laboratory reared *Physa pomilia* and *Pseudosuccinea columella* (a

lymnaeid) found that spawning occurred even when the snails had been maintained in total darkness.

Considering the entire spawning season, the number of eggs deposited per substrate per day was significantly greater ($P_o < 0.05$) in the intermediate distance category (Fig. 14). This distance category was apparently preferred for spawning sites, since the snails themselves had not been concentrated here (Fig. 8).

The effect of the interaction between date and distance from shore on the number of eggs deposited per substrate per day was significant ($P_o < 0.01$) (Fig. 14). That is, the major spawning period did not occur at the same time in the three distance categories, but was progressively later at greater distances from shore. There were, however, striking synchronies among distance categories in changes in oviposition rate (May 21 to 28), and the maximum spawning rates for all three categories occurred concurrently (May 24 to 26).

It was noted that the most abrupt rise and fall in oviposition rate (May 22 to 27, Fig. 14) had been paralleled by a similarly abrupt rise and fall in water temperature at thermograph Station A (APPENDIX VII). This suggested that changes in the water temperature might have significantly influenced the snails' motivation to spawn.

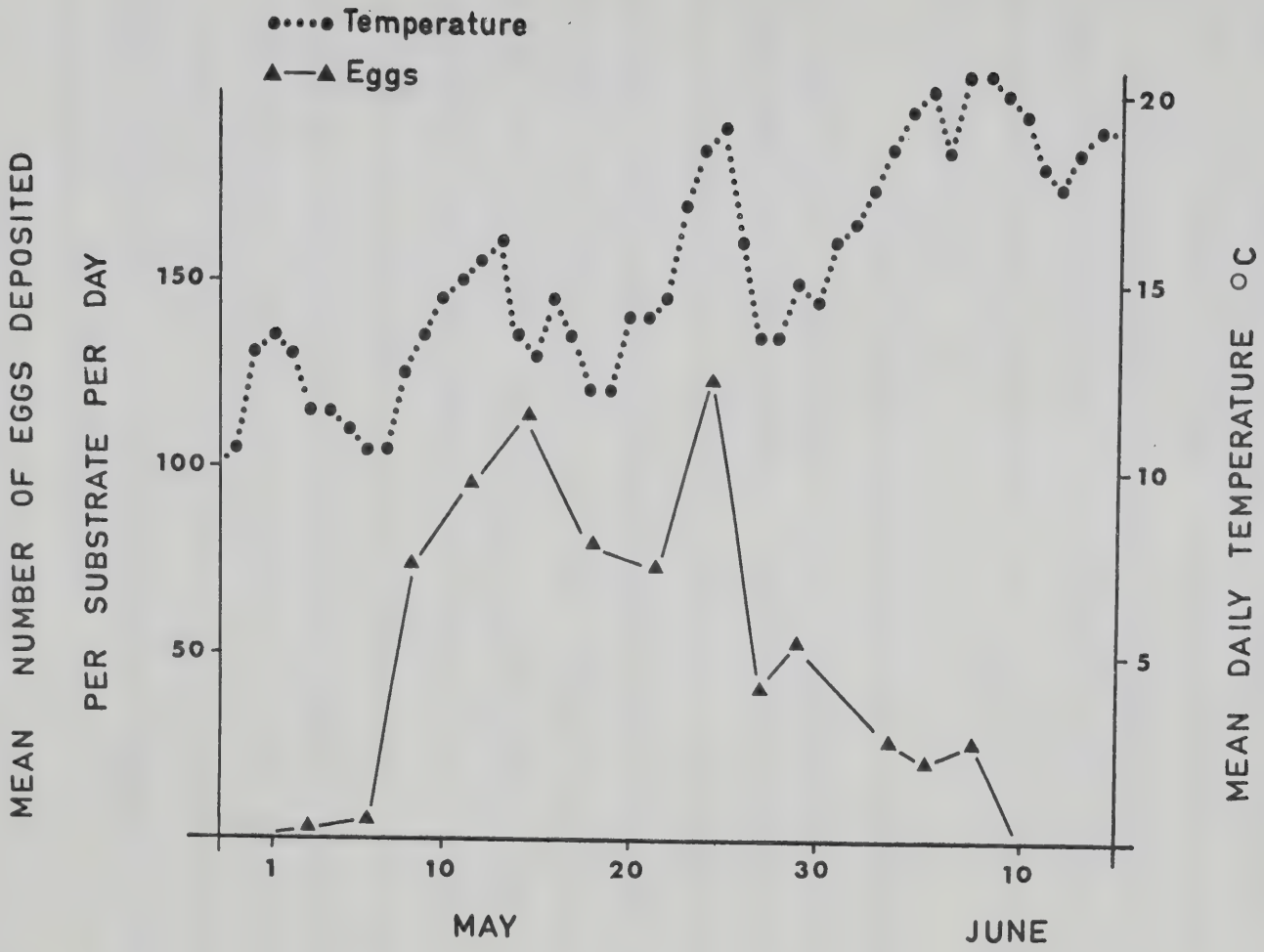
Jenner (1951) demonstrated that in *Stagnicola palustris* spawning was stimulated or suppressed by in-

creasing or decreasing water temperatures. Warming has been considered stimulatory to spawning in *Lymnaea spp.* (Van Nieuwenhoven and Lever, 1946; Precht, 1967, Van der Steen, 1967) and in *Australorbis glabratus* (Michelson, 1961).

It seemed likely that water temperatures near the substrates in the distance category closest to shore, where the water was relatively shallow, would have been comparable to temperatures at thermograph Station A, which was 15 inches below the water's surface. Such similarities were evident in the data recorded later in the summer (APPENDICES VI and VII). When the data on water temperature at Station A and the data on spawning rate in the first distance class were plotted together (Fig. 15), they were found to be very closely correlated up to about the end of May. It appeared that oviposition had not occurred before the water temperature had risen above about 10°C, and that above this level, rising temperatures had stimulated spawning, while falling temperatures had suppressed it.

Temperature data similarly applicable to the two deeper distance categories were not available. However, it seemed probable that the warming in spring of the water near the bottom of Clyde Pond had occurred more slowly at greater distances from shore. The progressively later occurrence of spawning at greater distances from shore

Figure 15. Mean daily water temperature at thermograph Station A (15 inches below the water's surface), and mean rates of spawning by *Helisoma trivolvis* on artificial substrates 1 to 4 (at the bottom of Clyde Pond, 1.0 to 5.5 feet from shore).


Temperature
Eggs
MEAN NUMBER OF EGGS DEPOSITED PER SUBSTRATE PER DAY
MEAN DAILY TEMPERATURE °C
150
100
50
20
15
10
5
1
10
20
30
10
MAY
JUNE

(p. 61) may thus have been merely another expression of the effect of temperature on spawning rate. Probably snails near the shore were periodically highly stimulated to spawn by intervals of rapidly increasing temperature. On the other hand, snails farther from shore probably experienced more consistent, but relatively mild levels of stimulation except on certain occasions, such as May 23 to 27 (Fig. 5).

It was unfortunately impossible to determine accurately the time at which eggs deposited on the Plexiglas substrates had hatched. Because new egg masses, like the Plexiglas itself, became encrusted with Aufwuchs within several days, egg masses which were a few days old appeared the same as those already hatched. More importantly, egg masses with embryos a few days from hatching, those just hatching, and those having dead embryos left inside, were also indistinguishable. In any future use, such substrates should be modified so that egg masses may be observed "from behind", through the Plexiglas. This could be accomplished by providing hinges along one side of the "box" which would allow it to be opened for inspection and for cleaning of the inner surfaces.

Because of the difficulty in seeing into egg masses, the numbers of infertile egg masses could not be accurately determined. Advanced embryos were observed, however, in over 90 per cent of egg masses deposited on the artifi-

cial substrates, and infertile egg masses were never encountered in the laboratory.

De Witt (1955) reported that sexually mature *Physa gyrina* were common in early fall and deposited some egg masses at this time. They were apparently snails hatched in the current season. Parallel observations have been reported for *Physa fontinalis* (De Wit, 1955; Duncan, 1959) and *Lymnaea stagnalis* (Jenner, 1951).

Coincidentally with the present study, evidence of late summer spawning by *Physa jennessi* and *Lymnaea stagnalis* was noted several times, but it was only found once in *Helisoma trivolvis*. *Helisoma trivolvis* egg masses were never found in Clyde Pond in late summer, but one out of 50 specimens removed to the laboratory on August 11, 1969 produced three small egg masses between August 15 and 20.

Several species of basommatophorans from the temperate zone reportedly continue oviposition, having once begun, as long as temperature and food supplies remain above critical levels, or until senescence occurs (Agersborg, 1932; Noland and Carriker, 1946; De Witt, 1967). *Helisoma trivolvis* brought into the laboratory on May 13, 1969, for the purpose of determining an average spawning rate, deposited egg masses almost as soon as the experiment began. But their spawning rate declined steadily thereafter, and by May 26 they had ceased spawning altogether. This indi-

cated, as was also becoming clear in the field, that the snails only continued oviposition until their clutch of eggs had been depleted (see Fig. 14 and p.70).

This conclusion did not exclude the possibility, suggested by the field data (p.62), that temperature effects could induce modifications of the basic reproductive rhythm. In the experiments carried out to investigate the effects of temperature in the laboratory, relatively few egg masses were deposited, and the result was weak data (Table 4). This occurred because the specimens had been collected unfortunately near the end of the spawning season, and because about one quarter of them had been castrated by trematode redia (see p.80). Nevertheless, *Helisoma trivolvis* kept at 13°C, maintaining the previously experienced decline of 6°C, (p.15), produced fewer egg masses by the end of May ($P_o < 0.05$) than those which were subjected to a temperature rise of 3°C (16°C) or 6°C (19°C). There were no statistically significant differences among the remaining treatment combinations ($P_o > 0.05$). The conclusions drawn from these results were that a temperature increase of 3°C was equally as stimulatory to spawning as an increase of 6°C, and that the temperature decrease of 6°C had depressed spawning.

None of the snails collected in June 1969 and held at 15° - 18°C or 22° - 25°C produced any egg masses within the seven month duration of the experiment. Thus,

Table 4. The numbers of new egg masses deposited following May 27 by groups of ten *Helisoma trivolvis* under conditions of increased or decreased temperature.

Date	Treatments							
	A		B		C		D	
	19°C - May 25 16°C - May 26 13°C - May 27 to June 3 16°C - June 4 to June 6		19°C - May 25 16°C - May 26 13°C - May 27 19°C - May 28 to June 3		19°C - May 25 16°C - May 26 13°C - May 27 16°C - May 28 to June 3		19°C - May 25 16°C - May 26 13°C - May 27 16°C - May 28 to May 31 19°C - June 1 to June 3	
Rep.	I	II	I	II	I	II	I	II
May 31	1	2	6	2	5	3	4	7
June 3	0	0	0	0	1	0	0	3
June 6	0	0	0	0	0	0	0	0

warm temperatures alone did not provide the conditions required for the resumption of spawning. Although evidence reported by Agersborg (1932) and De Witt (1967) have indicated otherwise, Precht (1967) and Jenner (1951) have demonstrated that long-day photoperiods may be necessary for spawning to occur in basommatophorans. Since the *Helisoma trivolvis* in this experiment were continuously exposed to photoperiods in excess of 15 hours, it was concluded that warm temperatures and a long photoperiod together were also insufficient to permit reproduction.

Since only one of the approximately 70 snails collected from mid-August to September deposited egg masses in the laboratory, it had seemed possible that the snails might require a period of cold, comparable to winter conditions, before they could respond to the stimulus of increasing water temperatures. But, of the snails collected on October 5, 1969, neither those subjected to cold (2° - 6°C or 0° - 3°C), nor those maintained at 18° - 19°C, produced any egg masses before March 1, 1970. Therefore, no evidence was obtained that cold treatment was required, and the conditions necessary for the completion of the reproductive cycle in *Helisoma trivolvis* remained unknown.

Reproductive maturation in basommatophoran gastropods has often been considered associated with growth beyond certain minimum sizes (Walton and Jones, 1926; Duncan, 1959; Hunter, 1961b; McCraw, 1961; Richards, 1962;

Berrie, 1966), but it has also been considered a function of age (Noland and Carriker, 1946; De Witt and Sloan, 1958; De Witt, 1967).

A few juvenile *Helisoma trivolvis* collected in 1968 were found to have well developed ovotestes (i.e. maximally prominent acini) and greatly distended seminal vesicles as early as August 13. These specimens all exceeded 11.0 mm in diameter. Among the other specimens recovered on the same date, all those over 9.0 mm in diameter had at least prominent acini, while smaller snails showed no more than the slightest evidence of maturation. The degree of distension of the seminal vesicles was considered indicative of the relative numbers of stored spermatozoa (Abdel-Malek, 1954). Thus, the "state of development" of the seminal vesicles was an index of the previous activity of the ovotestis.

Of 34 *Helisoma trivolvis* recovered on October 3, 1968, all of which exceeded 8.0 mm in diameter, 27 had well developed ovotestes and 18 of these had distended seminal vesicles. The albumen gland was not large in any of the snails, but it had become visible in 26. The specimens with poorly developed ovotestes were all under 9.3 mm in diameter, and none of these had distended seminal vesicles.

Snails of the 1968 generation were not collected again until May 16, 1969, but of the 30 specimens recovered,

three were still immature. The smallest snail in the collection (7.2 mm in diameter) showed the least advancement in maturity; its seminal vesicles were totally developed and its acini were barely discernable. The other two immature specimens, at 7.8 and 9.1 mm in diameter, had partially developed ovotestes and albumen glands, but lacked spermatozoa in the seminal vesicles. The remaining "mature" specimens had well developed ovotestes, seminal vesicles, and albumen glands, and averaged 11.8 mm in diameter.

It appeared, therefore, that with *Helisoma trivolvis* in Clyde Pond, maturation was correlated best with size (shell diameter), but the intervention by winter in the development of late hatching juveniles may have accounted for poor correlation with age.

In many of the adult *Helisoma trivolvis* collected in June and early July, the acini were barely visible and seminal vesicles were only slightly distended. Acini were prominent in all snails of comparable size collected at other times of the year, and their seminal vesicles were generally either moderately or greatly enlarged. These observations suggested that the spring spawning season was characterized by the release of accumulated ova and spermatozoa, and that much of the remainder of the year was characterized by gametogenesis. Since adult snails grew significantly only during the spawning season (p.29), nutrients consumed in excess of maintenance requirements at

other times of the year were apparently stored rather than expended. When mobilized at the time of egg production, these reserves probably became available to the entire animal, and growth became possible.

Mortality Factors

The abiotic factors considered as potential causes of mortality in *Helisoma trivolvis* were unseasonably high, low, or rapidly changing temperature and rapidly receding water levels.

Helisoma trivolvis did not die after being subjected in the laboratory to 0°C or to instantaneous changes in temperature of even 12°C. Since the temperature at thermograph Station A in Clyde Pond was never observed to vary more than 6°C in six hours (APPENDIX VII), rapidly changing water temperature was rejected as a possible mortality factor.

All snails which were frozen were killed by this treatment, and all had badly cracked shells. In Clyde Pond, snails located near the shore in winter no doubt were in danger of being killed in this way. Their late summer migration away from the shoreline (p.45) was possibly a behaviourial mechanism for minimizing this threat.

The upper limit of temperature tolerance was not specifically investigated in the laboratory since aquaria

occasionally reached 30°C without causing snail mortality, while pond temperatures never reached this level (APPENDIX VII).

Since *Helisoma trivolvis* was not generally distributed close to the water's edge (Fig. 8 and 9), it was not seriously endangered by receding water levels. They were only occasionally found trapped in water so shallow they could not move, and there was no evidence that the population decline in late summer 1968 (Table 3) was related to the abnormally rapid decline in water level between August 13 and 21 (p.14). The major population decline occurred between August 21 and 29, when, in fact, the water level was rising.

In the summer of 1968, many thousands of small fish were hatched and reared in Clyde Pond. After late June, one could scarcely look into the pond without seeing dozens of them. The brook stickleback *Culaea inconstans* predominated, but fathead minnows *Pimephales promelas* were also common. The stomach contents of some of the larger specimens of these fish, particularly the stickleback (collected on July 10), included up to three or four tiny *Helisoma trivolvis*. Most specimens had no snails in their stomachs, but rather large numbers of Tendipedidae larvae and cladocerans. Also, the extent of mortality arising from even such a dense fish population did not prevent the *Helisoma trivolvis* population from expanding during 1968

(p.39).

Both species of fish were totally absent from Clyde Pond in the summer of 1969, presumably as a result of dissolved oxygen depletion during the previous winter.

Tabanid larvae (Diptera) and some leeches have been considered enemies of snails (Pennak, 1954; Moore, 1966).

Chrysops mitis was the only tabanid whose larvae were present in Clyde Pond. Members of this genus are reportedly detritus feeders (Pennak, 1953), and the *Chrysops mitis* larvae maintained with snails did not attempt to attack them.

Several species of leeches were present in Clyde Pond. These were, in order of relative abundance, *Erpobdella punctata*, *Helobdella stagnalis*, *Nephelopsis obscura*, *Placobdella ornata*, *Glossiphonia complanata*, and *Haemopis marmorata*. *Helobdella stagnalis* (Moore, 1966), *Glossiphonia complanata* (Moore, 1964) and *Nephelopsis obscura* (Moore, 1912) have been reported to prey upon at least some snails, but none of the leeches listed above destroyed snails in the tests conducted in this study. *Helobdella stagnalis*, the only species so tested, attacked Tendipedidae larvae and oligochaetes without hesitation. It was concluded that snails were not a major prey of any of these leeches.

Ducks feeding on Clyde Pond, and observed through

binoculars, almost always ignored large snails (>10 mm in diameter), and only blue-winged teal were ever seen to eat them. Bartonek and Hickey (1969) have reported that ducks prefer small snails because they can be swallowed whole, or their shells easily crushed. Food habits studies have indicated that the blue-winged teal may be the only local duck for which snails are a preferred food (Collias and Collias, 1963; Dirschl, 1969; Sugden, 1969). In 1968, three blue-winged teal were seen on Clyde Pond continuously from mid-July to August 21. Possibly they had been attracted by the relatively abundant juvenile *Helisoma trivolvis* (Table 3). Such an attraction might also explain why these ducks were diving while feeding on August 13 and 21 only; the juvenile snails were at this time beginning to move away from the shore into deeper water (p.45). The absence of blue-winged teal from the pond after August 21 was ascribed to pre-season hunting.

Helisoma trivolvis in Clyde Pond was heavily infected by both the rediae (Fig. 16) and metacercariae of an echinostome trematode *Echinoparyphium recurvatum*. The life cycle of *Echinoparyphium flexum*, which may be synonymous with *Echinoparyphium recurvatum* (Senger, 1954), has been described by Najarian (1954).

The adult of *Echinoparyphium recurvatum* occurs in virtually all species of ducks present in Alberta (J. C. Holmes, personal communication). Thus, any duck

visiting Clyde Pond was potentially a source of *Echinoparyphium* eggs.

In the present study, one of two blue-winged teal (*Anas discors*) and a shoveler (*Spatula clypeata*) collected on Clyde Pond had *Echinoparyphium* in the small intestine. Also, infections were established in laboratory reared mallards (*Anas platyrhynchos*) and lesser scaup (*Aythya affinis*) by feeding each bird three or four *Helisoma trivolvis* containing several hundred to a thousand metacercariae in the kidney. Attempts to infect coots (*Fulica americana*) were unsuccessful.

Mallards, blue-winged teal, shovelers, American widgeon (*Mareca americana*), gadwalls (*Anas strepera*), and lesser scaup all used Clyde Pond, but usually only mallards, blue-winged teal or lesser scaup were present. Of these more common species, the blue-winged teal was probably an especially significant host because it alone utilizes snails as a preferred food (p.74).

Since the metacercariae of *Echinoparyphium* were present in the snails throughout the year, and since the mature parasite was obtained from laboratory reared birds (ducks or chicks of domestic fowl) seven or eight days after they had been challenged with metacercariae, ducks may have been seeding Clyde Pond with *Echinoparyphium* eggs throughout virtually the whole summer.

Echinoparyphium eggs which had been maintained

at 19 to 22°C began hatching about two weeks after they had been removed from the adult, and all had hatched within a few days. When maintained between 16 and 20°C, they did not begin hatching for three weeks, and had not completely hatched until after five weeks. In Clyde Pond, they probably developed even more slowly, particularly from autumn through spring, because of still lower water temperatures (Fig. 5).

In 1968, newly developing redial infections (i.e. those with few rediae) first appeared in Clyde Pond on August 13 in juvenile *Helisoma trivolvis* (Fig. 16 and 17). Although in 1968 no adult snails were collected after July, it seemed likely that they too had been infected. In 1969, of those snails collected which had been adults in 1968, 70 per cent were found to be harbouring rediae. These rediae were assumed to have developed from infections initiated in 1968, and not earlier, because no evidence was obtained from either field data (see Fig. 16, 1969) or laboratory experience (p.80) to suggest that snails infected by rediae could survive more than one year. Also, redial infections were produced consistently in adult *Helisoma trivolvis* exposed experimentally to *Echinoparyphium* miracidia.

The proportion of *Helisoma trivolvis* infected by the rediae of *Echinoparyphium* varied in Clyde Pond between zero and 34 per cent. This indicated that a regular programme of sampling is probably essential for any

Figure 16. The percentages of juvenile and adult *Helisoma trivolvis* found infected by *Echinoparyphium* rediae in Clyde Pond during 1968 and 1969.

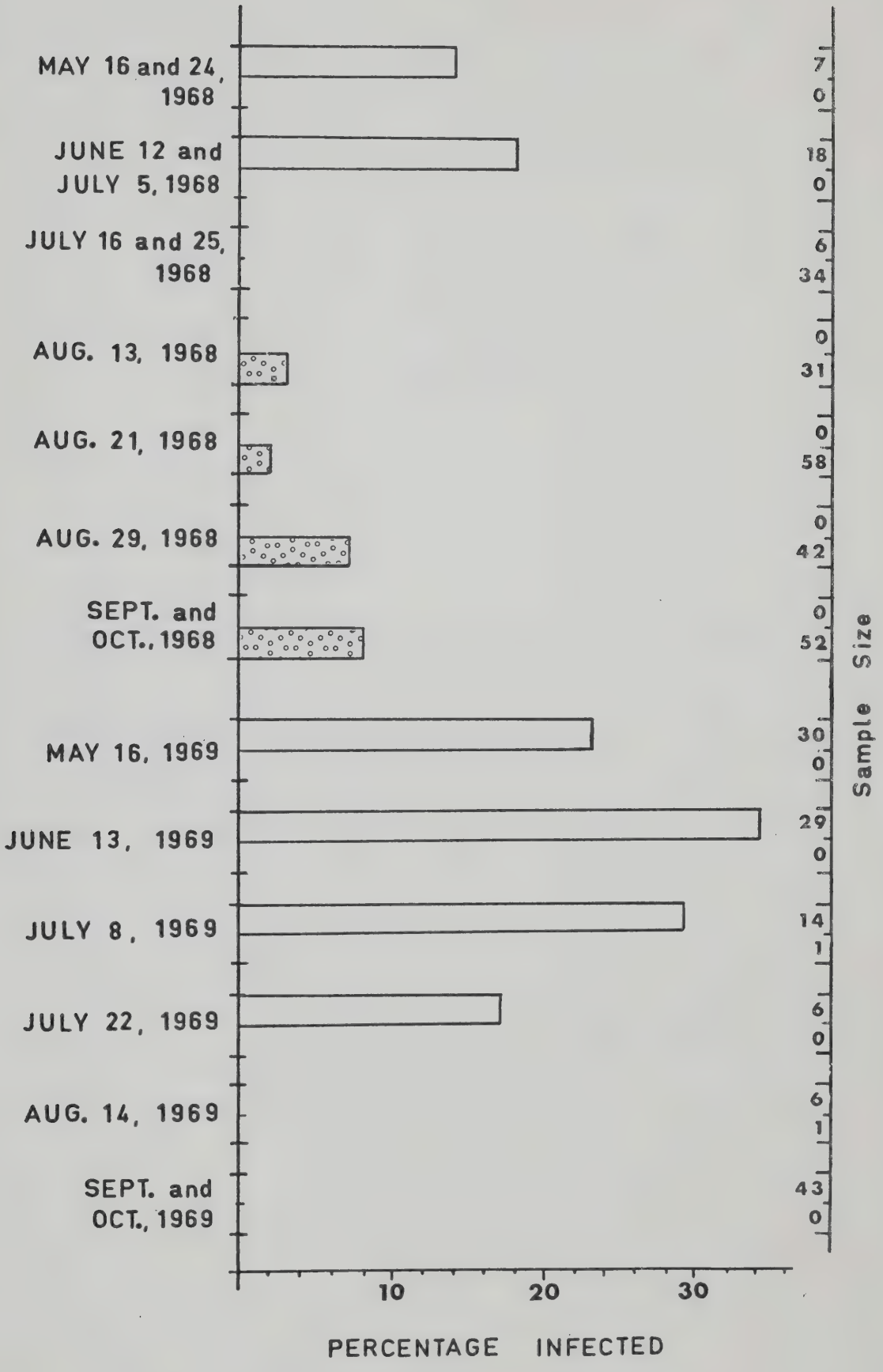
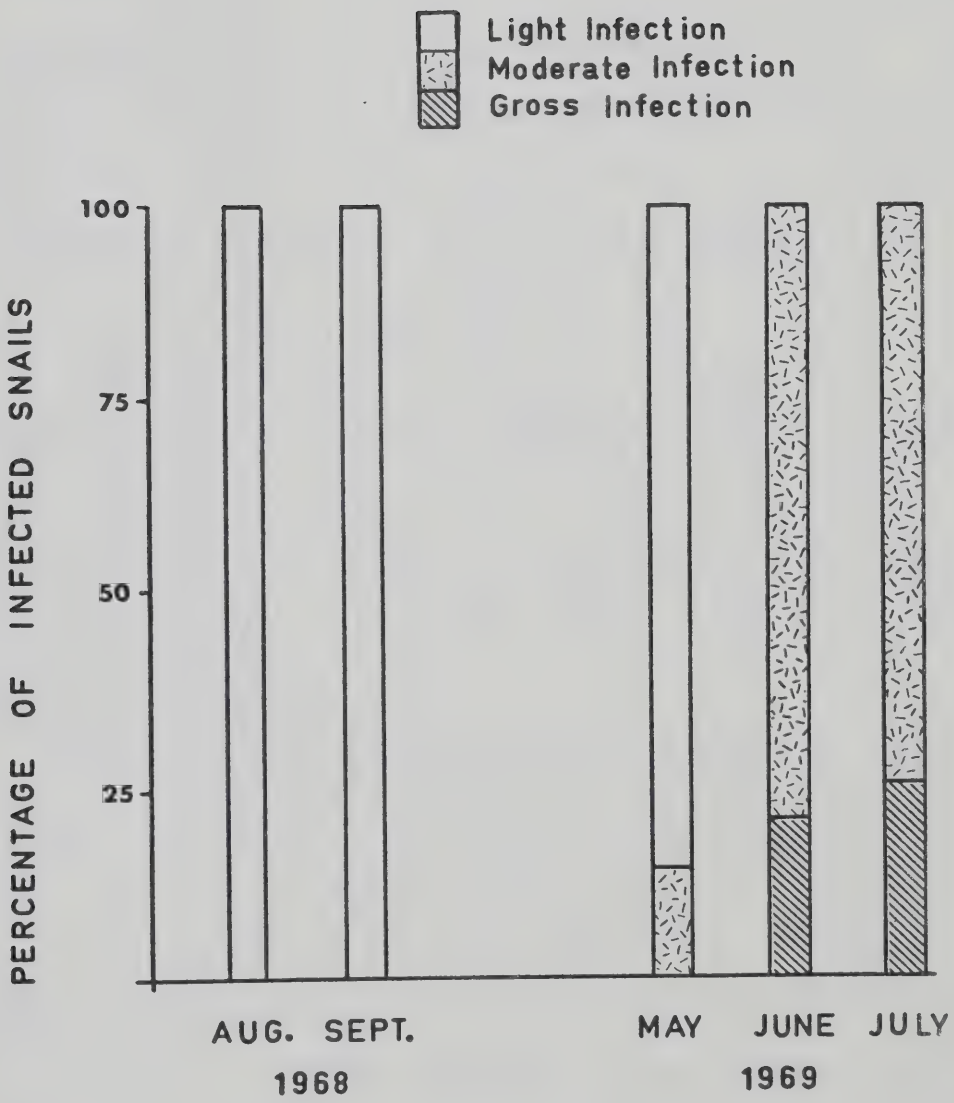

MAY 16 and 24, 1968
JUNE 12 and JULY 5, 1968
JULY 16 and 25, 1968
AUG. 13, 1968
AUG. 21, 1968
AUG. 29, 1968
SEPT. and OCT., 1968
MAY 16, 1969
JUNE 13, 1969
JULY 8, 1969
JULY 22, 1969
AUG. 14, 1969
SEPT. and OCT., 1969
10
20
30
PERCENTAGE INFECTED
Sample Size
7 0
18 0
6 34
0 31
0 58
0 42
0 52
30 0
29 0
14 1
6 0
6 1
43 0

Figure 17. Advancements in the severity of infection (relative numbers of rediae) of *Helisoma trivolvis* by *Echinoparyphium*, in Clyde Pond, from August 1968 to July 1969.


Light Infection
Moderate Infection
Gross Infection
PERCENTAGE OF INFECTED SNAILS
100
75
50
25
AUG. SEPT.
1968
MAY JUNE JULY
1969

reliable evaluation of the importance of such a parasite.

Changes in the rate of infection (Fig. 16) were largely ascribable to within-year variation, which appeared to follow an annual cycle. However, there were also important changes between years; in the latter part of 1969, for instance, no snails were infected by rediae, while about 8 per cent were infected at a comparable time in 1968. Also, the infection rate recorded in the spring and early summer may have been greater in 1969 than in 1968, but a statistically significant difference could not be demonstrated, possibly because sample sizes were too small in 1968.

The maximum rate of infection (34 per cent) slightly exceeded the published comparable values of which the author was aware. Cheng (1964) reported that 20 per cent of a collection of *Helisoma trivolvis* contained rediae of *Echinoparyphium sp.*, and Bourns (1963) found 23 per cent infection in *Lymnaea stagnalis*.

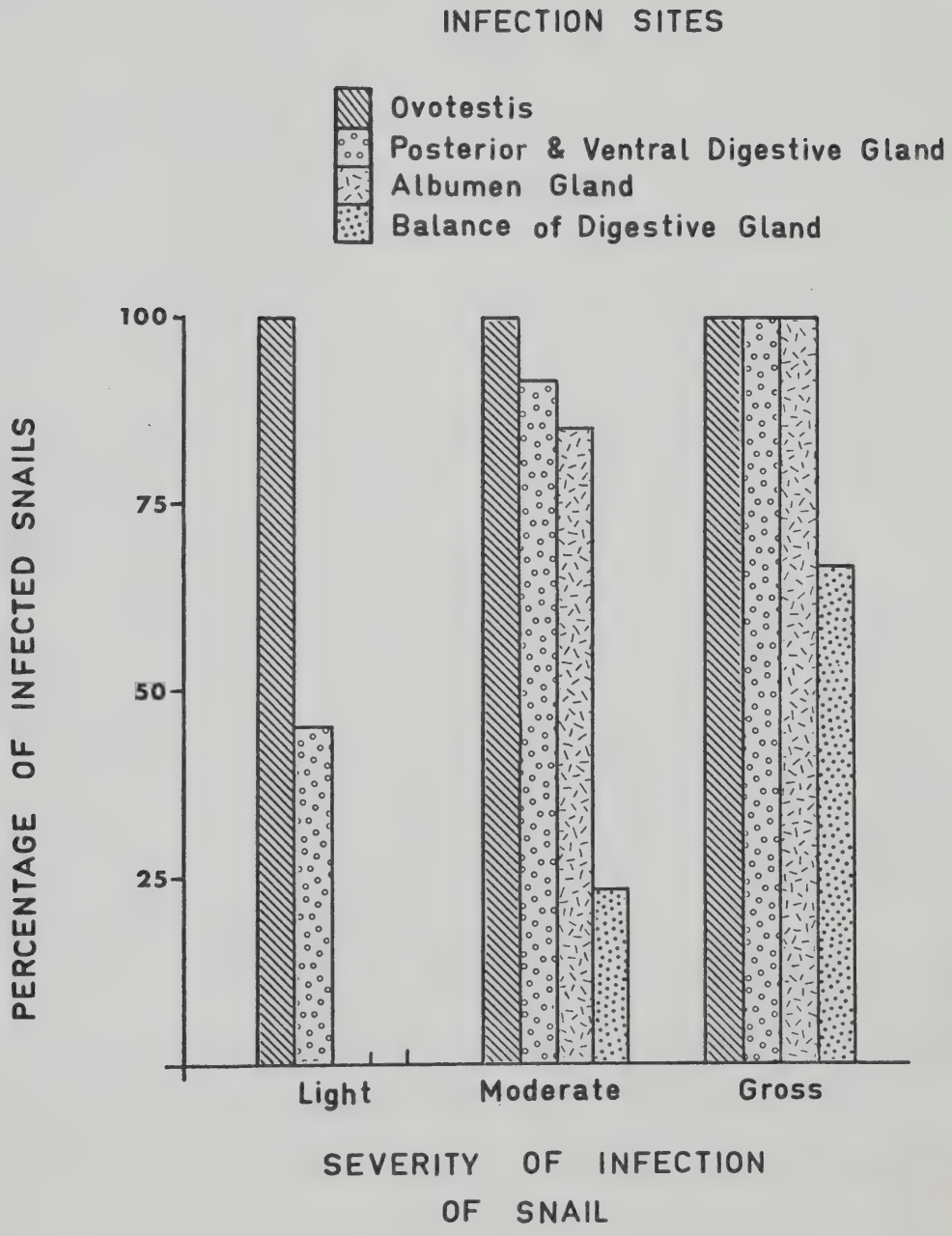
Wright (1966) generalized that trematode larvae rarely attack the gonad of molluscs as a primary site of infection, but that it may be invaded through "overspill" from gross infections of the digestive gland. However, the sites initially attacked by *Echinoparyphium* rediae in *Helisoma trivolvis* in Clyde Pond were the ovotestis, and, less regularly, the posterior and mid-ventral regions of the digestive gland, where the seminal vesicles and hermaphroditic duct were located. These were the only

areas invaded when rediae were few in number (Fig. 17 and 18), the only areas never free of rediae in infected snails (Fig. 18), and the only areas infected in August and September-October, 1968, when rediae were beginning to appear in the snail population.

Cheng (1963) reported that *Echinoparyphium* rediae were nourished primarily through ingesting the tissues of their host (*Helisoma trivolvis*), and that the digestive gland was the primary site of infection. In the present study, it was observed that the ovotestis, the albumen gland and the digestive gland were destroyed sequentially (Fig. 18), and the designation of a "primary" site of infection seemed inappropriate. *Echinoparyphium* apparently castrated *Helisoma trivolvis* early in the course of redial infections, thereby preventing the depletion of its host's reserves through spawning. By consuming the energy-rich albumen gland (McMahon, von Brand and Nolan, 1957) before inflicting any significant damage upon the digestive gland, a more vital organ, the parasite made relatively efficient use of its host's nutriments. Many *Helisoma trivolvis* were found to have survived until all but the last remnants of the digestive gland were destroyed. But infection by rediae apparently always resulted in the death of the snail.

It has been reported that larger snails may be proportionately more susceptible to miracidial infection than smaller snails, and that snail gigantism is correlated

Figure 18. The sequence of attack of infection sites in *Helisoma trivolvis* by *Echinoparyphium* rediae.


INFECTION SITES
Ovotestis
Posterior & Ventral Digestive Gland
Albumen Gland
Balance of Digestive Gland
PERCENTAGE OF INFECTED SNAILS
100
75
50
25
Light
Moderate
Gross
SEVERITY OF INFECTION
OF SNAIL

with the presence of rediae (Wesenburg-Lund, 1934; Rothschild, 1941). Among the juvenile *Helisoma trivolvis* recovered from dredge samples in 1968, *Echinoparyphium* rediae were found only in specimens over 9.4 mm in diameter, and the mean diameter of those infected was 11.3 mm. Also, the specimens containing rediae among 64 one-year-old *Helisoma trivolvis* collected from Clyde Pond on July 16, 1969,had been significantly larger ($P_o<0.01$) at the end of the previous summer than their uninfected counterparts (Fig. 19). Thus, either miracidia had tended to enter larger snails, or else snails which had been infected by miracidia tended to have higher growth rates.

Helisoma trivolvis infected by *Echinoparyphium* rediae grew significantly ($P_o<0.01$) more in 1969 than uninfected snails (Fig. 19). This was not associated with their size at the end of the previous summer, since within both infected and uninfected groups, the snails originally the largest had grown the least.

The specimens of adult *Helisoma trivolvis*, carrying *Echinoparyphium* rediae, which were collected in July, had not grown significantly more ($P_o>0.05$) than those collected in June (1969). Thus, as in uninfected snails (Fig. 6), growth had occurred primarily between May and June, and the greater total growth observed in parasitized snails probably resulted from an increased rate of growth during this time, rather than a prolongation of the growth

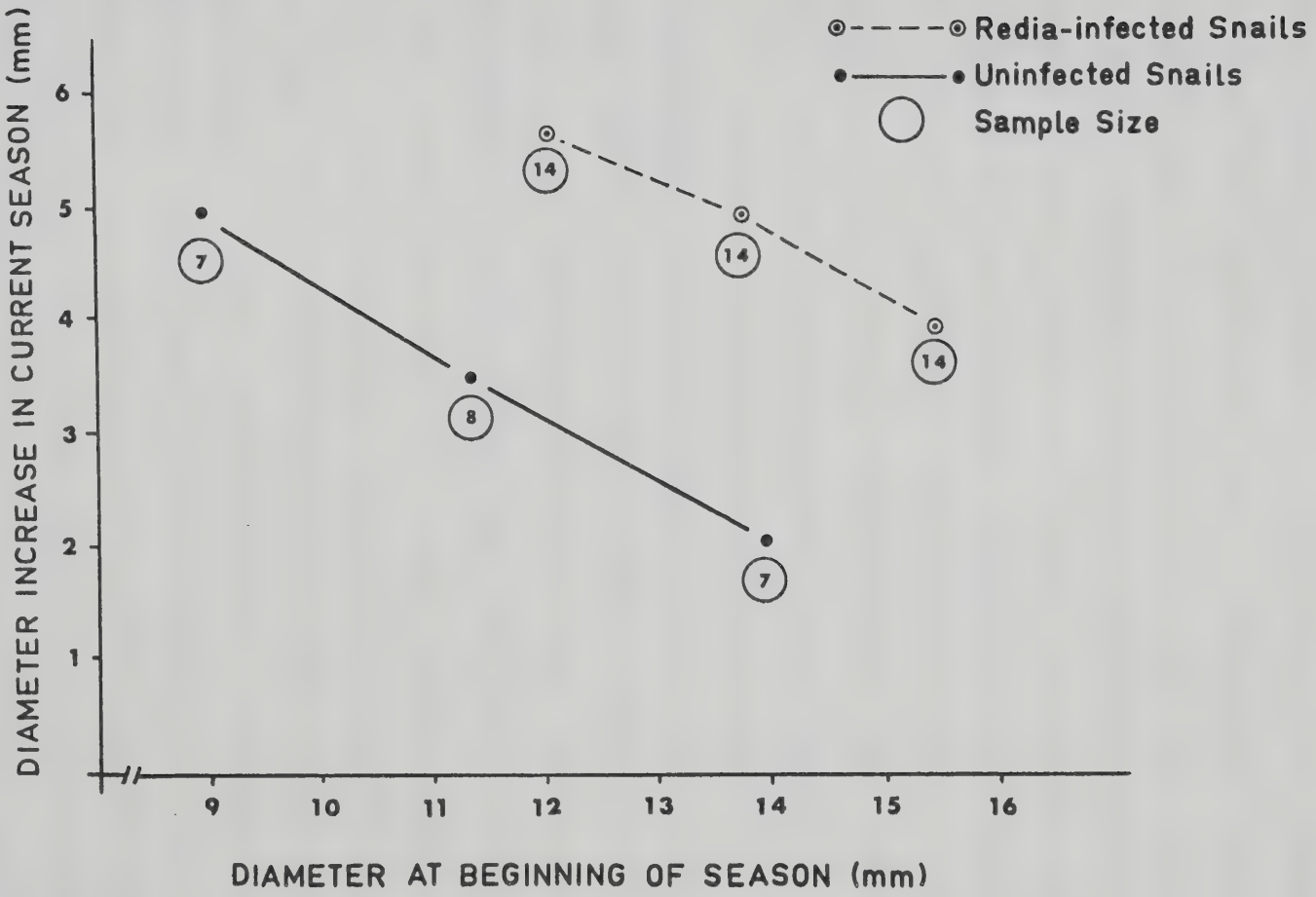
period.

Rothschild's (1941) hypothetical explanation of gigantism was that it is a result of parasitic castration, with the reserves normally utilized by the gonads being made available for general growth. This suggestion was supported by the present study, since a correspondence was revealed in adult *Helisoma trivolvis* between the time of shell growth and the time of spawning (see above), and since the rediae of *Echinoparyphium* invaded their host's reproductive system immediately before and during the spawning season (see p.80). In view of the fact that ducks tended not to eat large snails (p.74), to elicit gigantism may be beneficial to *Echinoparyphium*, through reducing the probability that a snail harbouring rediae would be destroyed prematurely.

The period during which cercariae were shed by *Echinoparyphium* rediae in *Helisoma trivolvis* was not investigated, but it probably began at about the time moderately intense redial infections were first observed (Fig. 17). A few free cercariae were found in dissected snails which were infected to this degree. No cercariae could have been released for long after all the snails with advanced redial infections had died (Fig. 16). Thus, cercariae were probably shed from mid-May to mid-July.

The infection of *Helisoma trivolvis* with *Echinoparyphium* metacercariae was remarkably complete.

Figure 19. The effect of parasitism by *Echinoparyphium* rediae on the growth of *Helisoma trivolvis* from early spring to July 16, 1969, in Clyde Pond.


Redia-infected Snails
Uninfected Snails
Sample Size
DIAMETER INCREASE IN CURRENT SEASON (mm)
1
2
3
4
5
6
14
14
14
7
8
7
9
10
11
12
13
14
15
16
DIAMETER AT BEGINNING OF SEASON (mm)

Not a single specimen over 5.0 mm in diameter was found uninfected, and adult snails often contained more than 1000 cysts. Virtually all metacercariae were found lodged close together at the nephrostome end of the snail's kidney, but a few were seen in the digestive gland of some redia-infected specimens. Immediately above the site where metacercariae encysted, a small area of the snail's mantle was free of black pigmentation. The size of this area was proportional to the relative numbers of metacercariae present, and, in heavily infected snails, a light-coloured spot was visible to the naked eye, even through the intact shell.

Metacercariae are considered to provoke little if any response from their snail hosts (Hurst, 1927, Wright, 1966). Indeed, many apparently healthy *Helisoma trivolvis* from Clyde Pond harboured large numbers of *Echinoparyphium* metacercariae, and they often survived as long in the laboratory as lightly infected specimens.

Such observations must be interpreted carefully, since they provide no information on deaths which may have occurred prior to the time of sampling, or under different conditions. In the case of this parasite, it seemed most unlikely that metacercariae (125 to 200 μ in diameter) could occupy the lumen of the kidney in newly hatched or very small species of snails without seriously impairing the kidney's performance.

The life cycle of *Echinoparyphium* was completed

in the laboratory from metacercaria to metacercaria, and the cercariae were studied the most carefully. These cercariae were sporadic swimmers and showed no apparent ability to locate snails, except by accidental contact. When a snail was encountered, the cercaria usually attached itself, using its suckers, and began creeping more or less aimlessly over the soft parts of its victim. Eventually, sometimes after creeping about for 20 minutes or more, the cercaria would arrive near the pneumostome. It then slowly manouvered its head into the pneumostome and, after a few seconds, pulled itself in one motion completely inside the pulmonary cavity. At the same instant, the tail was released, and the snail often was irritated in such a way that it opened the pneumostome.

In very small snails, it was possible to see through the shell and mantle and to observe the cercaria creeping about the interior of the pulmonary sac. They did not remain here, however, and from a few minutes to about two hours later they were visible at various locations in the kidney. Their entry into the kidney was never observed, but they may have entered via the ureter, which opens just within the pneumostome (Hyman, 1968:588).

The cercariae were usually encysted by five or six hours after entering the pneumostome, but the location of encystment was not always the kidney. In fact, in small snails, *Physa jennessi* and *Stagnicola palustris*

2 - 4 mm long, most of metacercariae were found in the pericardial cavity. (*Helisoma trivolvis* of comparable size unfortunately were not available.) Since in one instance, a metacercaria had lodged in the narrow renopericardial canal (the metanephridium), it was concluded that the cercariae had entered the pericardial cavity via this channel.

Where several metacercariae were present in the pericardial cavity, the movements of the heart were restricted. This interference with the functioning of the heart, and the observed blockage of the metanephridium, suggested other mechanisms (see also p.85) by which the metacercariae of *Echinoparyphium* could become a mortality factor. Their significance in *Helisoma trivolvis* was questionable, however, since metacercariae were not found in the pericardial cavity of specimens from Clyde Pond. Further investigation of this question is required.

Interspecific Interactions

Since the adult population of *Helisoma trivolvis* in Clyde Pond usually consisted largely of individuals recruited in the previous year (p. 31), the virtually complete failure of recruitment in 1969 (p. 41) was of profound significance.

This failure had not resulted from inadequate

spawning since there were significantly more adult snails present in May 1969 than in May 1968 (p. 39), and since large numbers of egg masses had been deposited on both natural and artificial substrata in 1969 (p. 58). Also, there was no evidence to suggest that the hatchability of eggs had been low in 1969 (p. 64). Therefore, since no empty shells of juvenile *Helisoma trivolvis* were collected in 1969 (Fig. 9), it was concluded that the juvenile snails had suffered a catastrophic mortality sometime before they had grown to 2.0 mm in diameter.

On the basis of the fact that juvenile snails were first collected in early July in 1968 (Fig. 9), and because the spawning season had ended earlier in 1969 than in 1968 (Fig. 11 and 14), it was concluded that the major loss of juveniles in 1969 had occurred before the end of June.

Major mortality had occurred among juveniles during this period in 1968 also, and the same agents of mortality may have been involved in both years. In 1968, 280 eggs were recovered per snail in dredge samples collected on May 24 (APPENDIX IX and Fig. 11), and the Abundance Index for eggs on this date was approximately 4200. If this value is considered a conservative estimate of total egg production in 1968, and if the maximum Abundance Index reached by juveniles over 2.0 mm in diameter is taken as 200 (see Table 3), over 95 per cent

of the juveniles must have died in 1968 before they attained 2.0 mm in diameter. Thus, there was an increase in the mortality rate of newly hatched juveniles between 1968 and 1969 of less than 5 per cent.

Since adult *Helisoma trivolvis* survived the month of June 1969 proportionately more successfully than juveniles (Fig. 8 and 9), it was apparent that the agent killing the juveniles was much less effective on the older and larger snails. This (see p. 85) and the other data available were entirely compatible with the possibility that this agent had been the metacercariae (or cercariae) of *Echinoparyphium*. *Helisoma trivolvis* hatched during the same period that cercariae were being shed (p. 83), and they were killed while very small (p. 88). The abundance of adult snails was probably at least 50 per cent greater in the spring of 1969 than in 1968 (Table 3), and the percentage of those infected by *Echinoparyphium* rediae also may have been higher in 1969 (Fig. 16); thus, the number of cercariae released in 1969, and therefore the probability of juvenile snails being infected, was much greater than in 1968. Furthermore, the single juvenile *Helisoma trivolvis* collected on July 8, 1969 (APPENDIX IX) had approximately 40 metacercariae in its kidney, while specimens of comparable size collected on July 16, 1968, had carried a maximum of four.

If, as implied above, the mortality rate among

newly hatched *Helisoma trivolvis* was a function of the numbers of *Echinoparyphium* cercariae present in the pond, then the factors influencing the abundance of cercariae require examination. Obviously, the number of snails available for infection by miracidia would be of major importance, and generally, this number would be a reflection of the level of recruitment of snails in the current season (Fig. 7). The percentage of the available snails actually infected by rediae would likewise be critical. This parameter would be directly proportional to the number of *Echinoparyphium* eggs entering the pond during the previous season, and this in turn would be proportional to the numbers of snail-eating ducks using the pond and the degree of infection of these birds by *Echinoparyphium*. Here again the level of snail recruitment probably would exert a major influence, since blue-winged teal may be attracted by concentrations of young snails (p. 74), and since the degree of infection of the ducks would be a function of the number of snails eaten. (Recall (p. 84) that the vast majority of *Helisoma trivolvis* examined carried numerous metacercariae.) Thus, it appeared that the lack of recruitment of *Helisoma trivolvis* in 1969 may have been caused by a negative-feedback, acting through blue-winged teal and *Echinoparyphium*, from the relatively high density of juveniles in 1968.

Through the mediation of snail-eating ducks, as explained above, the percentage of juvenile *Helisoma*

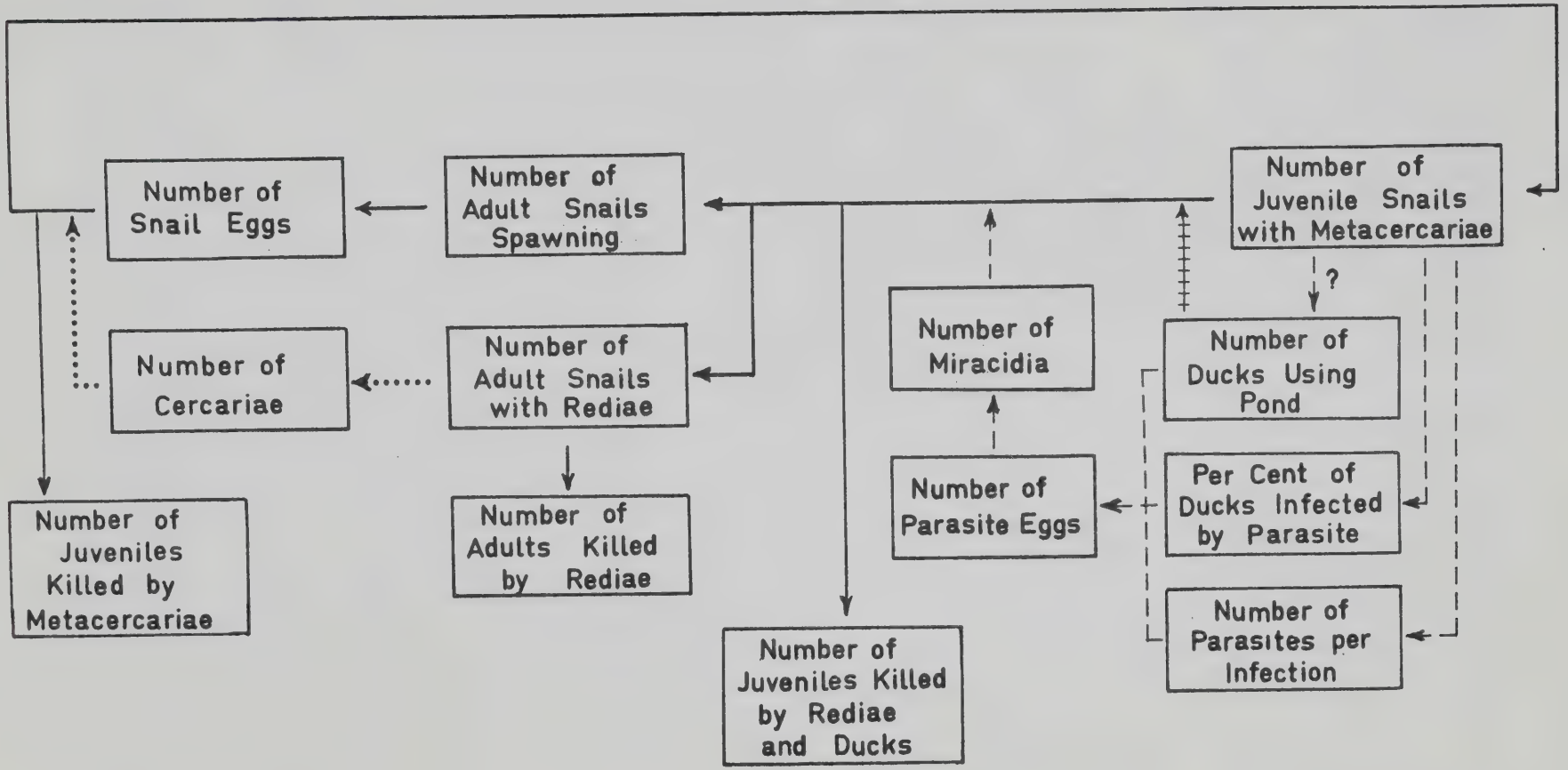
trivolvis that become infected by *Echinoparyphium* rediae may be proportional to their own density. Therefore, since the snails infected are castrated (p. 80), the mean number of eggs deposited per snail in the following spawning season may be inversely proportional to the density of juveniles.

Echinoparyphium rediae probably also cause some mortality of juveniles in the same season as they are infected. In Clyde Pond, the density of empty shells of juveniles had increased (p. 45) during the same period in 1968 as that in which the density of living juveniles had declined (p. 41). And this period also corresponded with the time of appearance of new redial infections (Fig. 16). Possibly even a few rediae could produce enough stress in these relatively small snails to cause their death.

The more significant of the possible interactions among *Helisoma trivolvis*, *Echinoparyphium* and blue-winged teal are summarized in Fig. 20.

If the metacercariae of *Echinoparyphium* may strongly reduce recruitment into relatively dense populations of *Helisoma trivolvis*, this might benefit the snail through preventing the overpopulation of its habitat. It is conceivable that the parasite also would benefit, in the long term, if it is true that denser populations of snails are characteristically more completely infected by rediae (pp. 39 and 79). Under such conditions, if

Figure 20. Postulated interactions among *Helisoma trivolvis*, *Echinoparyphium* and blue-winged teal, through which the level of recruitment of *Helisoma trivolvis* may be depressed.


Number of Snail Eggs
Number of Adult Snails Spawning
Number of Juvenile Snails with Metacercariae
?
Number of Cercariae
Number of Adult Snails with Rediae
Number of Miracidia
Number of Ducks Using Pond
Number of Juveniles Killed by Metacercariae
Number of Adults Killed by Rediae
Number of Parasite Eggs
Per Cent of Ducks Infected by Parasite
Number of Parasites per Infection
Number of Juveniles Killed by Rediae and Ducks

juveniles could not be killed by metacercariae, a density of snails could possibly be reached at which 100 per cent would become infected by rediae. Since redia-infected snails could neither spawn nor recover from infection, the populations of both the snail and the parasite would expire.

The fluctuations in the abundance of snails observed during this study (Table 3), and the age-composition of the adult population in 1968 (Fig. 7), suggested that the density of *Helisoma trivolvis* may have been oscillating with a frequency of about three years. Huffaker (1958) showed that a predator-prey system would not spontaneously produce oscillations in their densities unless some segments of the prey population were unavailable to the predator at any point in time. He achieved this situation by forcing the prey to live as several imperfectly isolated sub-populations. In Clyde Pond, oscillations in the densities of *Helisoma trivolvis* and *Echinoparyphium* may have been generated because only the newly hatched segment of the snail population was ever "available to" (i.e. able to be killed by) metacercariae. The snail population could be severely reduced, but the few older snails within it would survive to begin repopulating the habitat. The *Echinoparyphium* population would also survive, since metacercariae would be harboured in the older snails.

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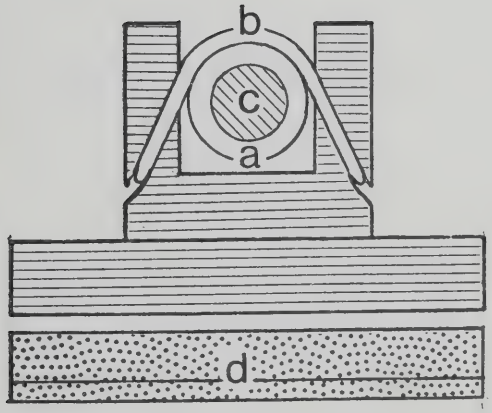
APPENDIX I. A schematic longitudinal section of the water sampler indicating the essentials of its operation, and an end view showing the method of securing the syringe.

a. Barrel of syringe
b. Rubber bands holding syringe
c. Plunger of syringe
d. Slide
e. Rubber band
f. Cord
g. Messenger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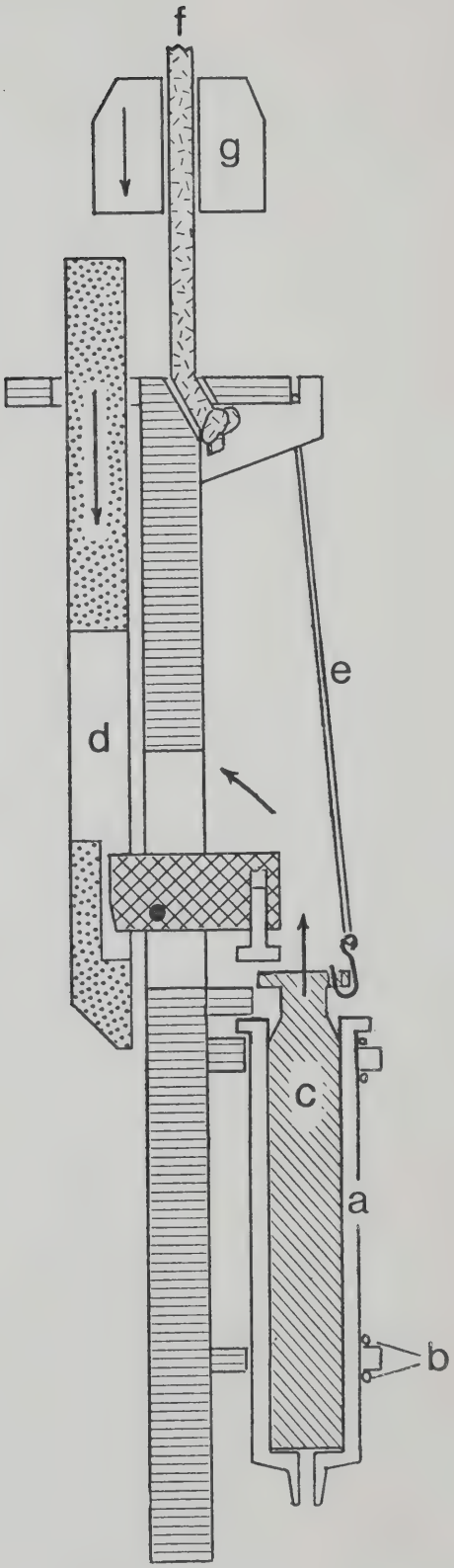
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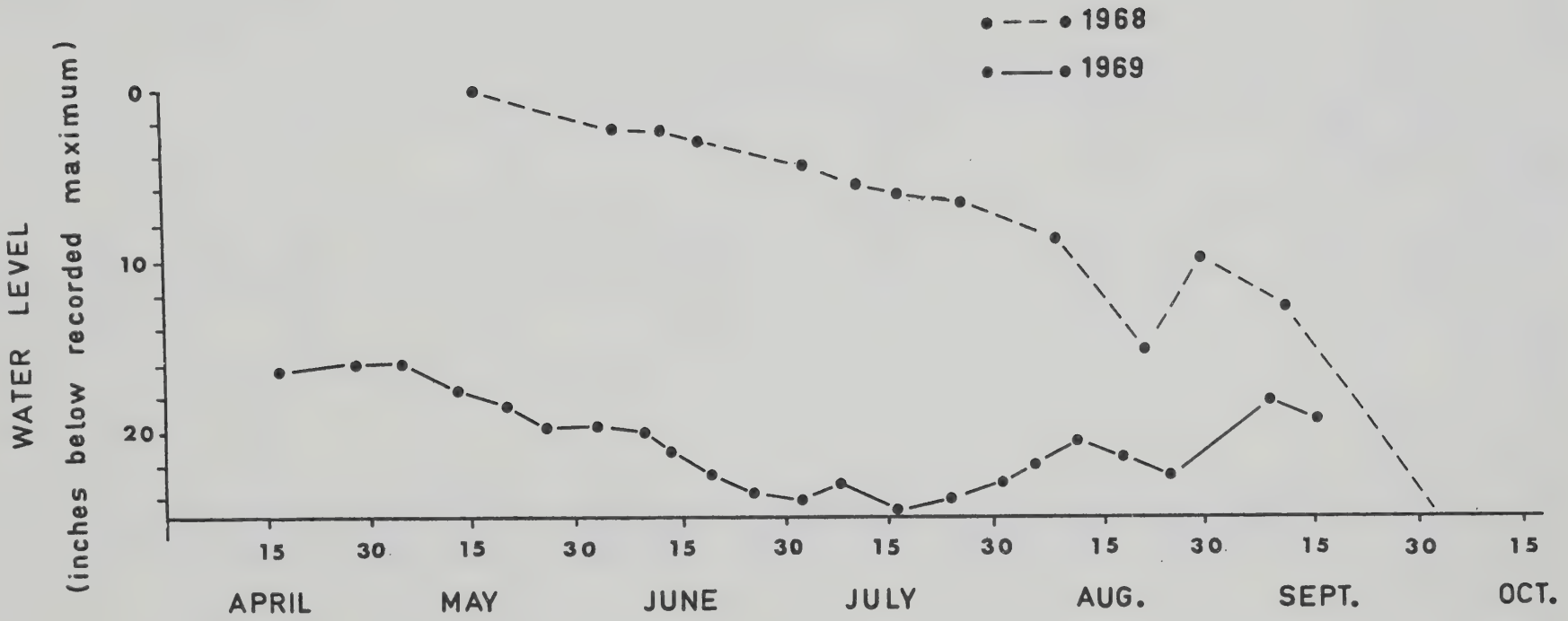
APPENDIX II. Fluctuations in water level in Clyde Pond between mid-May, 1968, and mid-September, 1969.


1968
1969
WATER LEVEL
(inches below recorded maximum)
0
10
20
15
30
15
30
15
30
15
30
15
30
15
30
15
APRIL
MAY
JUNE
JULY
AUG.
SEPT.
OCT.

APPENDIX III. Dissolved oxygen determinations from the middle of Clyde Pond, 1968.

Date	Time	Depths (feet)	O_2 Concentration (p.p.m.)	Percent Saturation
May 16	1600	Surface	12.0	128
		1	12.0	128
		2	12.0	128
		3	12.0	128
		4	12.0	128
		5	12.0	128
		5.5	12.0	128
July 16	1500	Surface	7.6	95
		1	7.2	89
		2	7.2	89
		3	7.2	87
		4	7.1	86
		5	7.0	84
July 25	0430	Surface	9.9	121
		1	9.9	121
		2	9.9	121
		3	9.9	121
		4	9.9	121
		5	3.0	36
	1200	Surface	9.9	123
		1	9.9	122
		2	9.9	122
		3	10.0	123
		4	9.3	113
		5	4.4	53
	1900	Surface	10.4	129
		1	10.4	130
		2	10.4	130
		3	10.4	129
		4	9.9	120
		5	5.9	70
August 29	1200	Surface	11.6	135
		1	11.6	135
		2	11.5	133
		3	11.4	132
		4	9.7	112
		4.2	8.7	101
October 3	1300	Surface	16.2	149
		1	- -	- -
		2	- -	- -
		3	- -	- -
		3.8	14.6	134

APPENDIX IV. Calcium hardness, pH and snail fauna in a series of artificial ponds near Fox Creek, Alberta.

Pond Number	Calcium Hardness (as $CaCO_3$) ppm	pH	*Lymnaea*	*Physa*	*Gyraulus*	*Helisoma*
27	23	9.7	P	A	P	A
22	30	9.9	P	A	P	A
2	35	8.7	P	P	P	A
3	35	9.6	A	A	P	A
24	35	8.7	P	A	P	A
15	40	9.1	A	P	P	A
18	40	9.6	P	A	P	A
37	45	9.4	P	A	P	A
16	50	9.1	A	A	P	A
17	50	8.8	P	A	P	A
28	50	9.4	P	A	A	A
31	50	9.2	P	A	A	A
34	50	9.4	A	A	P	A
1	55	8.9	P	A	P	A
9	55	8.9	P	A	P	A
23	55	9.4	P	P	A	P
30	55	8.6	P	A	P	A
5	60	8.8	A	A	P	A
32	60	8.9	P	A	P	A
21	65	8.5	A	A	A	A
6	70	8.8	A	P	A	A
39	70	9.4	A	P	P	A
29	75	8.7	A	A	A	A
19	80	8.7	A	A	A	A
20	80	8.5	A	P	P	A
35	80	8.7	P	A	P	A
4	85	8.4	A	A	P	P
7	85	8.6	P	A	A	A
40	85	8.7	A	A	A	A
8	85	8.6	P	P	A	A
12	95	8.5	A	P	A	A
11	100	8.4	A	A	A	A
36	100	10.1	P	A	P	A
10	110	8.7	A	A	A	A
33	110	8.9	P	A	P	A

P = present; A = absent

APPENDIX V. Vertical temperature gradients in Clyde Pond; recorded in the mid-pond region in 1968 and beside the thermograph stations in 1969.

Date	Time	Water depths (feet)						
		Surface	1	2	3	4	5	>5
1968								
May 14	1500	12.0	11.5	11.5	11.5	11.5	11.5	11.5
16	1600	12.5	12.5	12.5	12.5	12.5	12.5	12.5
17	1200	13.5	13.5	13.5	13.5	13.0	13.0	13.0
24	1400	17.0	17.0	17.0	17.0	17.0	16.5	
June 12	1300	16.0	18.0	18.0	18.0	18.0	18.0	
June 17	1200	16.0	16.0	16.0	16.0	16.0	16.0	
July 2	1200	19.0	18.0	17.0	16.0	15.0	14.5	
5	1100	23.0	23.0	23.0	23.0	23.0	18.5	17.5
16	1500	20.0	20.0	19.5	18.5	18.5	18.5	
25	0730	19.5	19.5	19.5	19.5	19.5	18.5	
	1330	20.5	20.0	20.0	20.0	19.5	19.0	
	2000	20.0	20.5	20.5	20.0	19.0	18.0	
Aug. 13	1100	16.5	16.5	16.5	16.5	16.0	16.0	
21	1200	17.0	16.5	16.5	16.5	16.0		
29	1200	17.0	17.0	16.5	16.5	16.5		
Sept.11	1100	16.0	16.0	15.5	15.5	15.0		
Oct. 13	1300	7.0	7.0	7.0	7.0	7.0		

APPENDIX V. Continued

Date	Time	Water Depths (feet)				
		Surface	1	2	3	>3
1969						
April 17	1100	0.0	0.0	0.0	0.0	0.0
28	1400	10.0	10.0	10.0	10.0	10.0
May 1	1400	14.0	14.0	13.0	12.0	10.5
23	1030	16.5	16.0	15.5	15.0	14.5
26	1200	15.5	16.0	16.0	16.0	16.0
28	1200	12.5	12.5	12.5	12.0	12.0
30	1300	14.5	14.0	14.0	14.0	13.5
June 2	1200	17.0	17.0	17.0	17.0	16.5
4	1200	20.0	19.0	19.0	18.5	18.0
6	1200	19.0	18.5	18.5	18.0	17.5
9	1200	21.0	21.0	21.0	20.5	19.5
11	1200	17.0	17.0	17.0	17.0	17.0
13	1200	18.5	18.5	17.0	17.0	16.5
13	1700	21.0	21.0	18.5	17.5	16.5
16	1600	21.0	21.0	19.5	19.0	18.0
19	1100	19.0	18.5	17.5	17.5	17.0
23	1200	19.0	19.0	18.5	18.0	17.5
25	1200	18.5	18.5	18.0	18.0	17.5
27	1200	24.0	22.0	18.5	17.5	17.5
July 2	1330	23.5	23.0	18.0	17.0	17.0
8	1330	20.5	17.5	16.5	15.5	15.5
16	1200	21.0	16.5	16.0	15.5	
22	1230	21.0	18.0	17.5	16.0	
24	1200	24.5	22.0	19.0	17.0	
31	1030	23.0	18.0	16.0	15.5	
Aug. 5	1100	18.0	18.0	18.0	18.0	17.5
7	1200	25.0	21.0	18.0	17.0	16.0
11	1200	21.0	19.5	19.0	18.5	17.0
18	1100	16.0	16.0	15.0	14.0	14.0
25	1200	19.5	16.0	15.0	15.0	14.5
Sept. 1	1200	18.5	15.0	14.5	13.5	13.5
9	1000	15.5	13.5	12.0	11.0	11.0
15	1500	9.5	9.0	8.5	8.5	8.5
Oct. 5	1400	8.0	--	--	--	6.0

APPENDIX VI. Bottom temperatures in Clyde Pond recorded at selected distances from shore (adjacent to artificial substrates). Distances from shore and water depths apply to June 11, 1969.

Date	Time	Water Temperatures (°C)										
		Distance from shore	1.5'	3.0'	4.5'	6.0'	7.5'	9.0'	10.5'	12.0'	13.5'	15.0'	16.5'
		Water Depth	3"	8"	13"	19"	24"	28"	32"	36"	42"	43"	45"
		Substrate	2	3	4	5	6	7	8	9	10	11	12
June													
11	1200		18.0	18.0	18.0	17.5	17.5	17.0	17.0	17.0	17.0	17.0	17.0
13	1200		19.5	19.0	17.5	17.0	17.0	16.5	16.5	16.5	16.5	16.0	16.0
	1700		22.0	21.0	20.0	19.5	17.5	17.5	17.0	17.0	17.0	17.0	16.0
16	1630		22.0	21.0	20.0	19.5	19.0	18.5	18.5	18.0	18.0	18.0	18.0
19	1100		20.0	19.5	18.5	18.0	18.0	18.0	17.5	17.5	17.5	17.0	17.0
23	1200		19.0	19.0	18.5	18.0	18.0	18.0	18.0	17.5	17.5	17.0	17.0
25	1200		20.0	19.0	18.0	18.0	18.0	17.5	17.0	17.5	17.0	16.5	16.5
27	1200		---	22.5	22.5	19.0	18.5	18.0	---	---	17.5	---	16.5
July													
2	1130		---	21.5	19.5	18.5	18.0	18.0	17.5	17.0	16.5	16.5	16.0
8	1330		---	19.0	17.5	17.0	16.5	16.0	16.0	16.0	15.5	15.5	15.5
16	1200		---	21.5	17.0	16.5	16.0	16.0	15.5	15.5	15.0	15.0	15.0
24	1200		---	23.0	23.0	20.5	19.5	18.5	18.0	17.5	17.0	17.0	16.5
31	1030		---	19.5	18.0	17.0	16.5	16.0	16.0	17.0	15.5	15.5	15.5
Aug.													
5	1100		---	18.5	18.5	18.5	18.0	18.0	17.5	17.0	16.5	16.0	16.0
7	1200		---	21.0	19.5	18.5	17.0	17.0	16.5	16.5	16.0	16.0	15.5
18	1100		---	16.0	15.0	15.0	14.5	14.5	14.0	14.0	14.0	14.0	14.0

APPENDIX VII. Water temperatures (°C) in Clyde Pond at four times of the day for thermograph Station A during the period April 28 to September 15, 1969. Station A was 15 inches below water surface at about 12 feet from shore.

Date	Time of day				
	0600 hrs	1200 hrs	1800 hrs	2400 hrs	Mean
April 28			10.0	9.5	
29	9.0	10.0	12.0	11.0	10.5
30	10.0	14.0	15.0	13.0	13.0
May 1	11.0	13.0	16.0	13.5	13.5
2	12.0	13.0	14.5	13.5	13.0
3	11.5	11.0	12.0	11.0	11.5
4	10.5	11.5	13.5	11.5	11.5
5	10.5	11.0	11.5	10.5	11.0
6	9.0	10.5	12.0	10.0	10.5
7	8.5	10.0	13.0	11.5	10.5
8	10.0	13.0	15.0	13.0	12.5
9	11.5	13.5	15.0	14.0	13.5
10	12.0	15.0	16.5	14.5	14.5
11	13.0	15.0	16.5	15.0	15.0
12	13.5	16.0	17.0	15.0	15.5
13	14.0	16.5	18.5	15.5	16.0
14	14.5	13.5	14.5	12.0	13.5
15	11.5	14.0	13.5	11.5	13.0
16	11.0	16.0	17.0	13.5	14.5
17	11.5	14.5	15.0	12.0	13.5
18	11.0	13.5	13.0	11.0	12.0
19	10.5	13.5	13.0	11.0	12.0
20	11.5	13.5	16.5	13.5	14.0
21	11.5	14.0	16.0	15.0	14.0
22	13.5	14.5	16.5	14.5	15.0
23	13.5	17.0	20.5	18.5	17.0
24	16.5	16.0	21.0	19.5	18.5
25	18.0	18.0	20.5	18.5	19.0
26	17.0	15.5	15.5	15.5	16.0
27	14.5	13.5	13.5	13.5	13.5
28	12.0	13.0	15.0	14.5	13.5
29	14.0	15.5	15.5	15.0	15.0
30	14.0	14.0	15.0	14.5	14.5
31	13.5	15.0	19.0	17.0	16.0
June 1	15.5	16.0	17.0	17.0	16.5
2	16.0	17.0	18.5	18.0	17.5
3	17.0	18.0	19.5	19.0	18.5
4	18.5	19.0	20.5	20.0	19.5
5	19.0	21.0	20.5	19.5	20.0
6	18.5	18.5	19.5	19.0	18.5
7	17.0	20.5	23.0	20.5	20.0
8	18.5	20.5	23.0	21.0	20.5
9	19.5	21.0	20.0	19.5	20.0
10	18.0	19.0	21.0	20.0	19.5
11	18.0	18.0	18.5	18.0	18.0
12	16.0	17.0	19.0	17.0	17.5

APPENDIX VII. Continued

Date	Time of day 0600 hrs	1200 hrs	1800 hrs	2400 hrs	Mean
June 13	16.0	18.0	20.5	19.5	18.5
14	17.0	19.0	21.0	19.5	19.0
15	16.5	19.5	21.0	19.5	19.0
16	18.5	19.5	20.5	19.5	19.5
17	18.5	19.5	20.5	- -	19.5
18	- -	- -	- -	- -	- -
19	- -	18.5	20.0	18.5	18.5
20	17.0	19.0	19.5	18.0	18.5
21	16.5	18.5	21.0	20.5	19.0
22	18.5	19.0	19.5	18.5	19.0
23	18.0	19.0	19.5	18.5	18.5
24	17.0	18.0	21.0	18.5	18.5
25	16.5	18.5	21.0	19.5	19.0
26	17.0	21.0	22.0	20.0	20.0
27	18.0	21.0	23.0	20.0	20.5
28	18.5	20.0	20.5	19.5	19.5
29	18.5	20.0	19.5	18.5	19.0
30	17.0	17.0	19.0	18.5	18.0
July 1	16.5	19.5	20.0	20.0	19.0
2	18.5	19.0	21.0	21.5	20.0
3	20.0	19.0	18.5	18.0	18.5
4	17.0	17.0	19.5	18.0	18.0
5	16.5	17.0	18.0	18.0	17.5
6	16.0	16.5	16.0	15.5	16.0
7	15.0	15.5	17.0	17.0	16.0
8	16.0	16.5	18.0	18.0	17.0
9	16.5	19.0	21.0	21.0	19.5
10	19.5	24.5	23.5	21.0	22.0
11	18.5	19.5	21.5	19.5	19.5
12	17.0	18.0	19.5	18.5	18.0
13	16.5	16.0	18.5	17.0	17.0
14	16.0	16.0	17.0	17.0	16.5
15	15.5	16.0	17.0	17.0	16.5
16	15.5	16.5	17.0	19.0	17.0
17	17.0	18.5	19.5	18.5	18.5
18	16.5	18.5	20.0	19.5	18.5
19	17.0	18.5	20.5	20.5	19.0
20	18.5	21.0	20.5	18.5	19.5
21	17.0	17.0	19.5	19.0	18.0
22	17.0	18.0	20.0	19.5	18.5
23	18.0	19.0	20.5	20.5	19.5
24	19.5	21.0	22.0	20.5	21.0
25	19.5	19.0	18.0	18.0	18.5
26	16.5	16.5	19.0	19.5	18.0
27	18.0	18.5	19.5	20.5	19.0
28	18.5	19.5	19.5	19.0	19.0
29	18.5	17.0	16.5	16.5	17.0
30	15.5	16.5	18.0	19.0	17.0
31	17.0	18.5	19.5	18.5	18.0

APPENDIX VII. Continued.

Date	Time of day				
	0600 hrs	1200 hrs	1800 hrs	2400 hrs	Mean
Aug. 1	18.5	19.5	20.5	20.5	19.5
2	19.5	19.0	21.0	19.0	19.5
3	18.0	19.0	20.0	18.5	18.5
4	18.0	18.5	19.5	20.0	19.0
5	18.5	18.0	18.0	17.0	18.0
6	16.0	16.5	18.5	19.5	17.5
7	18.5	20.0	19.5	19.5	19.5
8	19.5	20.0	22.5	21.0	20.5
9	20.5	21.0	22.5	22.0	21.5
10	20.0	19.5	20.0	19.5	19.5
11	18.0	19.0	22.5	20.0	19.5
12	19.0	18.5	18.0	17.0	18.0
13	16.0	18.0	18.5	18.5	17.5
14	17.0	18.5	18.5	18.0	18.0
15	18.0	18.0	19.0	17.0	18.0
16	16.5	15.5	15.0	15.0	15.5
17	14.0	14.0	15.0	15.5	14.5
18	15.5	15.0	19.0	17.0	16.5
19	16.0	15.5	16.0	15.5	16.0
20	15.0	16.0	18.5	17.0	16.5
21	15.5	15.5	16.0	15.5	15.5
22	14.5	15.0	16.0	15.5	15.5
23	15.0	16.0	16.0	16.0	16.0
24	15.5	16.0	19.0	16.5	17.0
25	15.5	16.0	17.0	16.5	16.5
26	16.0	15.5	16.5	16.5	16.0
27	15.0	15.5	15.5	15.5	15.5
28	15.0	15.5	15.5	15.0	15.5
29	14.5	15.0	15.5	15.0	15.0
30	14.5	14.5	15.5	15.0	15.0
31	14.0	14.5	15.0	15.5	14.5
Sept. 1	15.0	15.0	15.5	15.5	15.5
2	15.0	15.5	17.0	15.5	16.0
3	15.0	14.5	14.5	14.5	14.5
4	14.0	14.0	14.0	13.5	14.0
5	13.0	12.0	12.0	12.0	12.5
6	11.5	11.5	12.0	12.0	12.0
7	11.0	13.0	14.0	12.0	12.5
8	12.0	12.0	12.0	13.0	12.5
9	13.0	14.0	14.5	14.5	14.0
10	15.0	15.5	18.0	17.0	16.5
11	15.5	15.0	15.0	15.5	15.5
12	15.5	15.5	15.5	15.5	15.5
13	14.5	14.5	14.5	13.5	14.0
14	12.0	11.5	11.0	10.5	11.5
15	9.5	9.5	- -	- -	- -

APPENDIX VIII. Water temperatures (°C) in Clyde Pond at four times of the day for thermograph Station B during the periods June 19 to 26 and July 9 to August 18, 1969. Station B was at the bottom of the pond, about 12 feet from shore.

Date	Time of day				
	0600 hrs	1200 hrs	1800 hrs	2400 hrs	Mean
June 19	17.0	17.0	17.0	18.0	17.5
20	17.0	17.0	17.0	18.0	17.5
21	18.0	16.5	16.5	16.5	17.0
22	16.5	16.5	17.0	17.0	17.0
23	17.0	17.0	18.0	18.0	17.5
24	17.0	17.0	17.0	18.0	17.5
25	16.5	17.0	17.0	16.5	17.0
26	17.0	17.0	17.0	17.0	17.0
July 9	15.5	15.0	16.5	16.5	16.0
10	16.0	16.0	16.0	16.0	16.0
11	16.0	16.5	17.0	17.0	17.0
12	16.5	16.5	16.5	16.5	16.5
13	15.5	15.5	15.0	15.0	15.5
14	15.5	15.5	15.5	15.5	15.5
15	15.5	15.5	15.5	15.5	15.5
16	15.5	15.5	15.5	15.5	15.5
17	15.5	15.5	16.0	16.0	16.0
18	16.0	16.5	16.5	16.5	16.5
19	16.5	16.5	16.5	16.5	16.5
20	16.5	16.5	16.5	16.5	16.5
21	16.5	16.5	16.5	16.5	16.5
22	16.5	17.0	17.0	17.0	17.0
23	17.0	17.0	17.0	17.0	17.0
24	17.0	17.0	18.0	18.0	17.5
25	18.0	18.0	18.0	18.0	18.0
26	17.0	16.5	16.5	16.5	17.0
27	16.5	16.5	16.5	16.5	16.5
28	16.5	16.5	17.0	17.0	17.0
29	17.0	17.0	17.0	17.0	17.0
30	16.0	15.5	15.5	15.5	15.5
31	15.5	15.5	15.5	15.5	15.5
Aug. 1	15.5	15.5	16.0	16.0	16.0
2	16.5	16.5	17.0	17.0	17.0
3	17.0	17.0	17.0	17.0	17.0
4	16.5	16.0	16.0	16.5	16.5
5	16.5	17.0	17.0	18.0	17.5
6	17.0	16.5	16.0	16.0	16.5
7	16.0	16.0	17.0	16.5	16.5
8	16.5	16.5	16.5	16.5	16.5
9	16.5	16.5	17.0	17.0	17.0
10	17.0	18.0	18.0	18.0	17.5
11	18.0	18.0	18.0	18.0	18.0
12	18.0	17.0	17.0	17.0	17.5

APPENDIX VIII. Continued

Date	Time of day				
	0600 hrs	1200 hrs	1800 hrs	2400 hrs	Mean
Aug. 13	16.5	16.0	16.0	16.0	16.0
14	16.0	16.0	16.0	16.0	16.0
15	16.0	16.0	16.0	16.0	16.0
16	16.0	15.5	15.5	14.5	15.5
17	13.5	13.5	14.0	14.0	13.5
18	14.0	14.0	- -	- -	- -

APPENDIX IX. Numbers of *Helisoma trivolvis* recovered from dredge samples collected in Clyde Pond during 1968 and 1969. Juveniles were snails hatched in the current season while adults had survived at least one winter.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1968					
May 16	1	0	0	0	0
		3	0	0	0
		6	0	1	1
		9	0	1	1
		12	0	1	1
		15	0	0	0
		18	0	0	0
		21	0	0	0
May 24	1	0	0	0	0
		3	0	0	0
		6	0	0	0
		9	0	0	0
		12	0	0	0
		15	0	0	0
		18	0	0	0
		21	0	0	0
		24	0	0	0
		27	0	0	0
	2	0	0	0	0
		3	0	0	0
		6	0	4	4
		9	0	0	0
		12	0	0	0
		15	0	0	0
		18	0	0	0
		21	0	0	0
June 17	1	0	0	0	0
		1.5	0	0	0
		3	0	2	2
		6	0	0	0
		9	0	1	1
		12	0	0	0
		15	0	1	1
		18	0	0	0
		21	0	0	0

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1968					
June 17	2	0	0	0	0
		1.5	0	0	0
		4	0	0	0
		7	0	1	1
		10	0	0	0
		13	0	1	1
		16	0	0	0
July 2	1	0	0	0	0
		3	0	1	1
		6	0	0	0
		9	0	0	0
		12	0	0	0
		15	0	0	0
		18	0	0	0
	2	0	0	0	0
		2	1	0	1
		5	0	1	1
		8	0	0	0
		11	0	0	0
		14	0	0	0
		17	1	0	1
		20	0	0	0
July 16	1	0	0	1	1
		2	10	0	10
		4	14	0	14
		6	4	0	4
		8	6	1	7
		10	2	1	3
		12	0	0	0
		14	0	0	0
		35	0	0	0
	2	0	1	1	2
		2	38	0	38
		4	17	0	17
		6	7	0	7
		8	1	0	1
		10	0	0	0
		12	0	0	0
		14	0	0	0
		16	0	0	0

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1968					
July 25	1	0	0	1	1
		2	10	0	10
		4	7	0	7
		6	1	0	1
		8	2	0	2
		10	0	0	0
		12	3	0	3
		14	1	0	1
	2	0	0	0	0
		2	48	0	48
		4	38	0	38
		6	6	0	6
		8	7	0	7
		10	5	0	5
		12	1	0	1
	3	0	0	0	0
		2	15	0	15
		4	8	0	8
		6	5	0	5
		8	1	0	1
		10	2	0	2
		12	1	0	1
Aug. 13	1	0	5	0	5
		1.5	3	0	3
		3	15	0	15
		4.5	21	0	21
		6	2	0	2
		7.5	2	0	2
		9	0	0	0
		10.5	5	0	5
		12	5	0	5
	2	0	3	0	3
		1.5	14	0	14
		3	17	0	17
		4.5	18	0	18
		6	9	0	9
		7.5	7	0	7
		9	4	0	4
		10.5	4	0	4
		12	7	0	7
		13.5	5	0	5

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1968					
Aug. 21	1	0	2	0	2
		1.5	4	0	4
		3	2	0	2
		4.5	4	0	4
		6	7	0	7
		8.5	11	0	11
		10	8	0	8
		11.5	11	0	11
		13	1	0	1
		14.5	3	0	3
	2	0	0	0	0
		1.5	2	0	2
		3	3	0	3
		4.5	5	0	5
		6	6	0	6
		7.5	18	0	18
		9	1	0	1
		10.5	3	0	3
		12	1	0	1
		13.5	4	0	4
Aug. 29	1	0	1	0	1
		1.5	1	0	1
		3	1	0	1
		4.5	1	0	1
		6	2	0	2
		7.5	2	0	2
		9	5	0	5
		10.5	3	0	3
		14.5	1	0	1
		18.5	3	0	3
		22.5	0	0	0
	2	0	1	0	1
		1.5	3	0	3
		3	3	0	3
		4.5	0	0	0
		6	3	0	3
		7.5	5	0	5
		9	2	0	2
		10.5	5	0	5
		12	4	0	4
		13.5	1	0	1
		15	4	0	4

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1968					
Sept. 11	1	0	0	0	0
		2	0	0	0
		4	2	0	2
		6	2	0	2
		8	2	0	2
		10	0	0	0
		12	6	0	6
		14.5	2	0	2
		17.5	3	0	3
		35	0	0	0
Oct. 3	1	0	1	0	1
		1.5	2	0	2
		3	0	0	0
		4.5	1	0	1
		6	1	0	1
		7.5	0	0	0
		9	3	0	3
		11	27	0	27
		16.5	1	0	1
		26.5	0	0	0
		36.5	0	0	0
1969					
May 16	1	0	0	0	0
		1.5	0	1	1
		3	0	0	0
		4.5	0	1	1
		6	0	1	1
		7.5	0	2	2
		9	0	0	0
		10.5	0	1	1
		12	0	0	0
		13.5	0	0	0
		15	0	1	1
		16.5	0	1	1
		18	0	2	2
		19.5	0	1	1

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1969					
May 16	2	0	0	0	0
		1.5	0	1	1
		3	0	5	5
		4.5	0	4	4
		6	0	2	2
		7.5	0	0	0
		9	0	0	0
		10.5	0	1	1
		12	0	0	0
		13.5	0	1	1
		15	0	1	1
		16.5	0	1	1
		18	0	3	3
June 13	1	0	0	0	0
		1.5	0	0	0
		3	0	0	0
		4.5	0	4	4
		6	0	4	4
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	1	1
		13.5	0	0	0
		15	0	0	0
		16.5	0	0	0
	2	0	0	0	0
		1.5	0	1	1
		3	0	2	2
		4.5	0	2	2
		6	0	0	0
		7.5	0	1	1
		9	0	0	0
		10.5	0	0	0
		12	0	1	1
		12	0	1	1
		13.5	0	0	0
		13.5	0	1	1
		15	0	1	1
		16.5	0	0	0

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1969					
June 13	3	0	0	0	0
		1.5	0	1	1
		3	0	2	2
		4.5	0	2	2
		6	0	2	2
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		10.5	0	0	0
		12	0	1	1
		13.5	0	0	0
		15	0	0	0
		16.5	0	0	0
	4	0	0	0	0
		1.5	0	1	1
		3	0	0	0
		4.5	0	0	0
		6	0	1	1
		7.5	0	0	0
		9	0	0	0
		10.5	0	1	1
		12	0	0	0
		13.5	0	0	0
		15	0	0	0
		16.5	0	0	0
July 8	1	0	1	1	2
		1.5	0	0	0
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1969					
July 8	2	0	0	3	3
		1.5	0	0	0
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0
July 22	1	0	0	1	1
		1.5	0	0	0
		3	0	0	0
		4.5	0	2	2
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0
	2	0	0	2	2
		1.5	0	0	0
		3	0	1	1
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0
Aug. 14	1	0	0	1	1
		1.5	0	0	0
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	1	1

APPENDIX IX. Continued.

Date	Series	Distance to shore (feet)	Number of Snails Recovered		
			Juveniles	Adults	Total
1969					
Aug. 14	2	0	0	0	0
		1.5	0	0	0
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0
	3	0	0	0	0
		1.5	0	3	3
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	1	0	1
		13.5	0	0	0
	4	0	0	1	1
		1.5	0	0	0
		3	0	0	0
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0
Sept. 9	1*	0	0	0	0
		1.5	0	0	0
		3	0	1	1
		4.5	0	0	0
		6	0	0	0
		7.5	0	0	0
		9	0	0	0
		10.5	0	0	0
		12	0	0	0
		13.5	0	0	0

*Series 2,3, and 4, with samples collected at the same distances as in series 1, yielded no snails.

APPENDIX X. The numbers of new egg masses of *Helisoma trivolvis* deposited on Plexiglas substrates in Clyde Pond between inspection dates.

Oviposition Periods		Substrates											
		1	2	3	4	5	6	7	8	9	10	11	12
May	1-5	0	0	0	2	1	0	0	0	0	0	0	0
	6-7	0	2	0	0	1	1	0	1	0	0	0	0
	8-10	3	12	12	12	5	6	0	1	1	0	1	0
	11-13	4	12	13	9	3	13	11	0	0	1	0	0
	14-16	1	18	10	6	9	19	6	17	3	2	4	3
	17-20	-	8	7	11	14	35	23	20	12	9	11	3
	21-23	-	3	6	12	21	23	17	19	11	4	10	1
	24-26	-	5	16	16	29	19	29	30	22	18	35	24
	27-28	-	2	2	5	3	7	4	17	5	8	12	5
	29-30	-	1	3	7	5	8	11	12	5	15	17	13
	31-	-	4	1	8	5	14	4	2	6	17	18	19
June	2												
	3-4	-	1	3	2	5	8	7	1	6	3	8	3
	5-6	-	2	0	2	1	3	3	3	3	3	2	4
	7-9	-	2	5	2	1	6	1	2	2	2	2	0
	10-11	-	0	0	0	0	0	1	0	3	0	0	1

- Unavailable to snails.

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